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STUDIES OF CERTAIN COASTAL SAND DUNE PLANTS OF SOUTHERN CALIFORNIA

By

Edith A. Purer
San Diego, California

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STUDIES OF CERTAIN COASTAL SAND DUNE PLANTS OF SOUTHERN CALIFORNIA[1]

INTRODUCTION

The published literature on the vegetation of the coastal sand dunes of southern California is concerned with taxonomic matters and to a much lesser degree with successional relations. The present investigation deals with the autecology of some representative species of plants of this area. In addition certain environmental conditions have been studied, in order to determine under what general ranges of these important conditions this particular sand dune vegetation exists.

Method of Procedure

After a general survey of the sand dune areas of southern California, eleven representative species[2] were chosen, namely: *Abronia maritima* Nutt.,[3] *Abronia umbellata* Lam., *Atriplex leucophylla* Dietr., *Convolvulus soldanella* L., *Ericameria ericoides* (Less.) Jepson, *Eriogonum parvifolium* Sm., *Franseria bipinnatifida* Nutt., *Lupinus chamissonis* Esch., *Mesembryanthemum aequilaterale* Haw., *Oenothera cheiranthifolia* Hornem. var. *suffruticosa* Wats. (Munz, 1928), *Rhus integrifolia* B. and W.

The gross morphology of the roots, stems, leaves, flowers and fruits was investigated, and the subterranean and the aerial portions of the plant were measured and charted. Leaves, stems and roots were sectioned and variously stained for consideration of their anatomical structure. Certain habitat conditions under which the species grew were measured for fifty-six consecutive weeks.

Literature

Literature relating to the coastal sand dune areas of California is scanty. Reforestation problems received the attention of several individuals. Cooper (1922) refers to the development of coastal dunes in a brief paragraph and he has a comprehensive study of this strand vegetation in progress (Carnegie Institution Yearbooks, 1919, 1920, 1922). A quadrat study of an area in Los Angeles County was made by Couch (1914) while a floristic investigation was undertaken by Olsson-Seffer (1910) along the California coast. Abrams (1917) and Jepson (1925) have given in their manuals descriptions and distributions of sand dune species.

[1] This paper is part of a dissertation in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Southern California. The author's gratitude is especially due to Dr. H. de Forest, under whose direction this work was done, for his unfailing interest and encouragement. The coöperation of the other members of her committee is heartily appreciated. For the courtesies extended to her by the Dudley Herbarium of Stanford University and by the Herbaria of the University of California, Berkeley, and of the Academy of Sciences at San Francisco, the author is grateful.

[2] Hereafter when only the genus name is stated the particular species given below is implied.

[3] Jepson (1925) was followed in naming plants unless otherwise stated.

In other regions several comparative studies of sand dune plants have been made. Chrysler (1904) examining the leaf anatomy of plants growing on the Atlantic coast and on the shore of Lake Michigan found that:

(1) Plants growing in the maritime situation have thicker leaves than the same species growing inland, and (2) This increase in thickness of the leaf is always due, at least in part, to an increase in thickness of the palisade layer, and also (3) In some cases the number of palisade layers is increased in the maritime situation.

Starr (1912) makes the following statement:

Plants generally growing in mesophytic situations, when found also on the dunes, show the following modifications; *of the leaf,* increased thickness, decrease in depth and increase in surface-extent of the epidermal cells, increase in thickness of the outer wall of the epidermis and of the cuticle accompanied by ridging, increase in palisade, in hairs, in conductive and mechanical tissues; *of the stem,* decrease in the length of internodes, increase in the number of vessels and in the area of their cross-sections, giving greater conductive space, increase in thickness of the walls of vessels and of the fibers accompanied by decrease in lumen of fibers, giving more wood, increase in the number of rings in stems of a given size, showing slowness of growth, increase in mechanical tissues outside the wood, and increase in cork.

Harshberger found a number of modifications in the strand plants of the New Jersey coast (1909) and the sand dune plants of Bermuda (1908). An anatomical investigation of beach vegetation in the Philippines, to which references will be made later, was made by Kienholz (1926).

Waterman (1919)) states in his summary of "Development of root systems under dune conditions" that

These reactions are specific and hereditary, and may reflect the conditions under which the ancestral plants grew. They must be regarded as of great importance in the choosing of species for introduction into conditions where the humus content is uneven.

THE SAND DUNES

Locations and Their Extent

Several reconnaissance trips were made along the California and Oregon coasts from a point a short distance south of Descanso, Baja California, to Florence, Oregon. In southern California a long stretch of small dunes extends from Imperial Beach to Coronado in San Diego County. Holmes (1918) describes the coastal beach and dune sand of San Diego as a narrow strip bordering the ocean, rarely or never exceeding one-eighth mile in width and in places too narrow to map. The most striking development is the long sandy bar that partly encircles San Diego Bay. From there to El Segundo, Los Angeles County, there are merely occasional patches of dunes. Dunes,

however, are well developed at El Segundo. Not again until the northern limit of Santa Barbara County is reached, do large dunes appear.

The areas vary in size from a few acres to a number of square miles, and they may be continuous with the strand or superimposed upon bluffs. Some dune localities are separated from the mainland by bays, as for example, the Silver Strand in San Diego County, while others form a part of the mainland as at Guadalupe. Some of the regions are almost as low as the strand, while in other sections, usually farther from the ocean, the dunes may be over 100 feet in height, with troughs of actively blowing sand between them. Still farther north on the coast of California, and also of Oregon, large dune areas are active.

Areas for Investigation

Two areas in southern California were chosen for intensive study, namely: El Segundo in Los Angeles County, and the Silver Strand in San Diego County. These regions, some 130 miles apart, present not only the largest stretches of dunes in the southern part of the state, but are also representative of other dune areas along the coast of southern California and show a diversification of vegetation from early stages to late development.

Character

The sand dunes of California present one of the most dynamic of plant habitats. These regions, as in the case of the Lake Michigan dune studied by Cowles (1899), exhibit a number of distinct developmental stages. Among these the strand or beach at Pismo is notable, while at Guadalupe low foredunes are well developed just back of the strand. Moving dunes, a dune complex, and open stretches of sand of great instability and bearing little vegetation, occur at Hauser, Oregon. Near Monterey stabilization is well exemplified, vegetation approximating the climax of that region covering many old dunes. Various stages are exhibited at most of the dune areas.

These sand dunes are inhabited by a rather large number of plant species, over 100 being found on the Silver Strand and El Segundo areas. Growth-forms represented are perennial shrubs, including several species which may become trees elsewhere but are shrubs in the dunes; suffrutescent shrubs; evergreen perennial herbs with aerial portions which die annually; biennials; and annuals. There are species typical of the sand dunes, invaders from other surrounding communities, and ruderals. Pioneers in bare areas are those which are commonly sand dune species, while in later stages of the succession both sand dune species and others become components of the vegetation. About the edges of stabilized dunes ruderals compete with dune plants.

A portion of the vegetation has been disturbed both at El Segundo and at the Silver Strand, due to the construction of a highway and a railroad through the entire length of each area, interfering with succession and introducing ruderals.

Table 1 gives in a general way the coastal distribution of the eleven species studied. This has been ascertained through personal collections and the collating of range data accompanying specimens in the Dudley Herbarium, Stanford University, the herbarium of the California Academy of Sciences, San Francisco, and that of the University of California, in Berkeley.

ORIGIN

The sand dunes of coastal California are of recent geologic origin. Concerning San Diego County, Wiggins (1929) states:

> Along the immediate coast line the San Diego Formation is covered by a thin deposit of marine, littoral sand and silt, which constitutes the San Pedro Formation of the Pleistocene.

The beach deposits of Pliocene origin range from zero to fifty feet in depth. A lateral current passing southward along Point Loma, in San Diego County, and eddying below it, is the cause of the sand deposit on the Silver Strand.

As reported by Cooper (1927), the country adjacent to Monterey Bay and south of the Salinas River, covered by a complex of ancient dunes, is related to that period of uplift which characterized a portion of Pleistocene time.

The sand dunes are being built up by wind action from sand brought to the edge of the water by the action of the waves. Reed (1930) in examining sand at Playa del Rey, immediately north of El Segundo, found the sands derived from old rocks of the Santa Monica Mountains farther to the north.

TABLE 1. Coastal distribution of the 11 species.

States and Counties	Abronia maritima	Abronia umbellata	Atriplex	Convolvulus	Ericameria	Eriogonum	Franseria	Lupinus	Mesembryanthemum	Oenothera	Rhus
Washington	.	x[4]	.	x	.	.	x	.	.	.	.
Oregon	.	x	.	x	.	.	x	.	x	.	.
California											
Del Norte	.	x	.	.	.	.	.	.	.	.	.
Humboldt	.	x	x	x	.	.	x	.	x	.	.
Mendocino	.	x	.	x	.	.	x	.	.	.	.
Sonoma	.	x	.	.	x	x	.	x	.	.	.
Marin	.	x	.	.	.	.	.	x	.	.	.
San Francisco	.	x	.	x	x	.	x	x	x	.	x
San Mateo	.	x	x	x	.	.	x	.	.	.	.
Santa Cruz	.	x	x	x	x	.	x	x	.	.	.
Monterey	.	x	x	x	x	x	x	x	x	.	.
San Luis Obispo	x	x	x	.	x	x	x	x	x	.	.
Santa Barbara	x	x	x	x	x	x	x	x	x	x	x
Ventura	x	x	x	x	.	x	.	.	x	x	x
Los Angeles	x	x	x	x	x	x	x	x	x	x	x
Orange	x	x	x	x	.	x	x	.	x	x	x
San Diego	x	x	x	x	x[5]	x	x	.	x	x	x
Baja California	.	.	x	.	.	.	x	.	x	x	x

[4]x—Species present. [5]Collected in 1878.

ENVIRONMENTAL CONDITIONS

Plants are affected by both the atmospheric and the soil conditions under which they grow. Data concerning these factors were obtained for air temperature, precipitation, humidity, light, wind, soil moisture, soil character, soil temperature, and certain biotic factors.

Stations

For meteorological data on the two sand dune areas the San Diego and Los Angeles records of the Weather Bureau, U. S. D. A., were utilized.

Six stations in distinctive communities of different habitat conditions were maintained for fifty-six consecutive weeks, four at El Segundo and two on the Silver Strand. The following locations were selected: El Segundo, Los Angeles County—(1) On the strand, barely beyond the region of the severest storm waves, in small dunes caused by *Abronia maritima*. (2) On a moving dune, farther removed from the ocean, where there were small mounds of vegetation consisting principally of *Franseria bipinnatifida*. (3) On the lee slope of a stabilized dune. Of all the stations this was at the greatest distance from the ocean, where but little sand movement occurred. The principal species here was *Ericameria ericoides*. (4) In a large thicket of *Rhus integrifolia* which had been growing many years. Silver Strand Beach State Park, San Diego County. (5) On the strand, as at El Segundo, in small dunes caused by *Abronia maritima*. (6) In a large clump of *Rhus integrifolia* on an old stabilized dune near the bay side of the strand.

Evaporation

Data on evaporation were secured by means of the standardized Livingston non-absorbing, porous cup atmometers, those of both white and black types being employed. The atmometers were mounted by the Livingston and Thone (1920, 1924) methods. The instruments, in batteries of three white cups at each station, were sunk into the soil for about two-thirds of the height of the reservoir bottles. The evaporating surface of the cups was thus about 25 cm. above the surface of the sand. Weekly readings for each station were made for fifty-six consecutive weeks at the same time of day, never varying by more than an hour. The reservoir bottles were filled from a graduated burette to a file scratch on the neck. All the porous cups were restandardized once every three months, or oftener when deemed necessary (Livingston, 1915). When a restandardized cup was found to possess a new coefficient, the correction of its record was made on the basis that the difference between the new and the old coefficient did not prevail during the first one-third or one-fourth of its intervening record, and the difference was therefore distributed through the remaining two-thirds or three-fourths of that period.

These data (Figs. 1 and 2) show that the highest rates of evaporation occur in the region of the moving dunes and the next lower at the strand locations. In the more stabilized areas represented both by the Rhus stations (4 and 6) and the similarly located Ericameria station (3), the rates are considerably lower. Comparing two of the El Segundo stations it is to be noted that for the most part when the amount of evaporation increases at the Rhus station (4), it increases more rapidly at the Ericameria station (3), while in decreasing at each, it usually decreases slightly less at the Rhus station. Since the evaporation rates were obtained from the white porous cups and the evaporativity (Livingston, 1931) by means of the black porous cups, a fairly accurate idea may be gained of some of the conditions under which the plants live (Figs. 5 and 6).

AIR TEMPERATURE

Graphs of monthly mean maxima and minima (Figs. 3 and 4), were constructed from the records of the Weather Bureau, U. S. D. A., at Los Angeles and San Diego for the three years, January, 1930, to January, 1933. These data are adequate for the two areas in general, but cannot be applied to specific stations in each, where variations in temperature probably occur in dune topography with differing vegetative covers. Consideration of these records shows that there is a gradual rise in the summer with a gradual lowering in the winter months, the total yearly range being small. The range

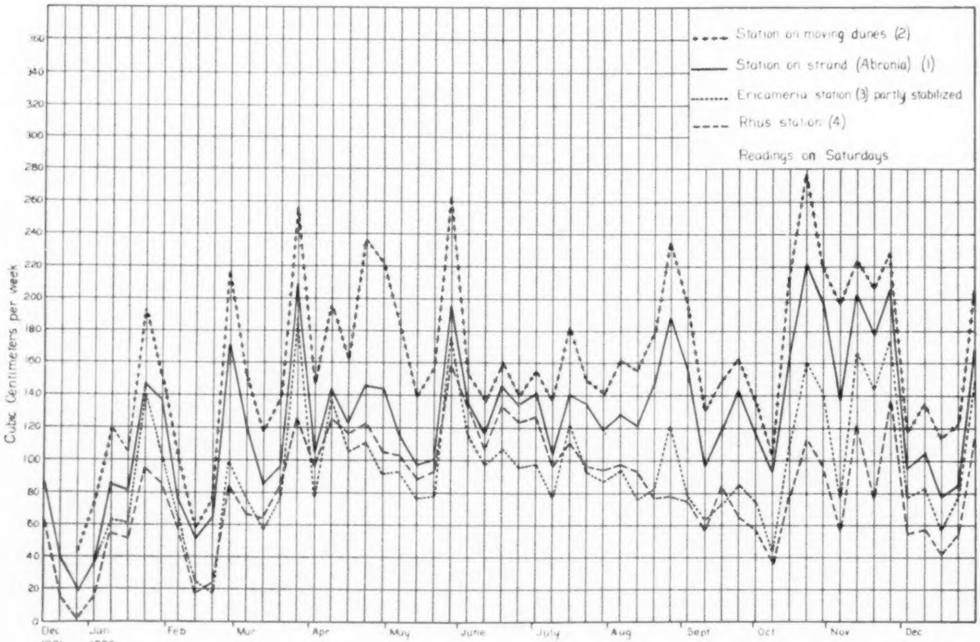

FIG. 1. Weekly evaporation El Segundo, Los Angeles County, December 12, 1931, to January 1, 1933, 56 weeks; Abronia Station (1), moving dune (2), Ericameria (3), and Rhus (4). Livingston white atmometer cups.

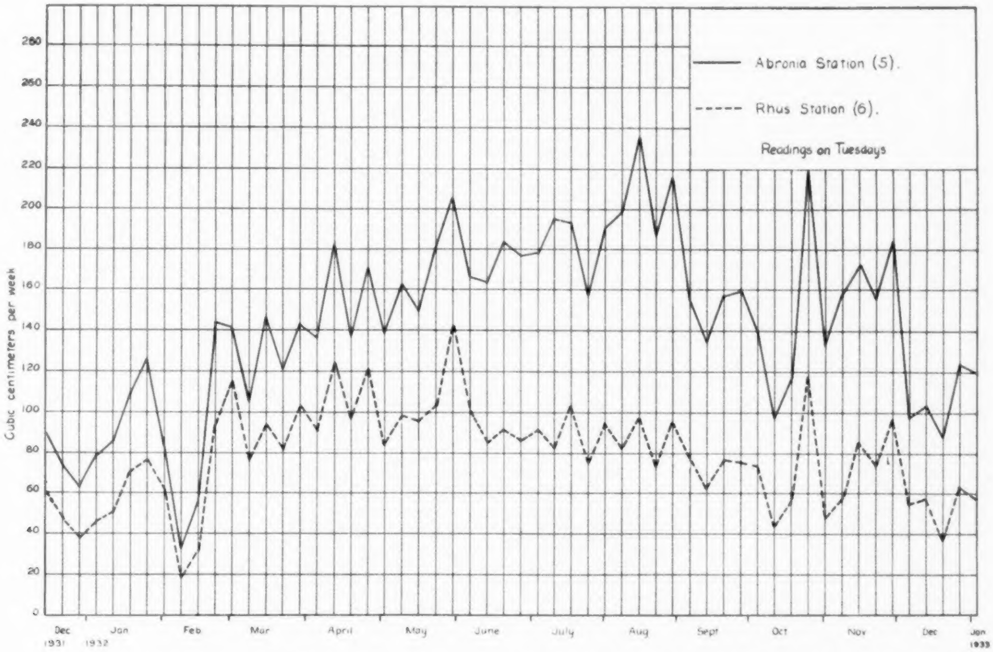

FIG. 2. Weekly evaporation Silver Strand, San Diego County, December 15, 1931 to January 3, 1933, 56 weeks. Abronia station (5), and Rhus station (6). Livingston white atmometer cups.

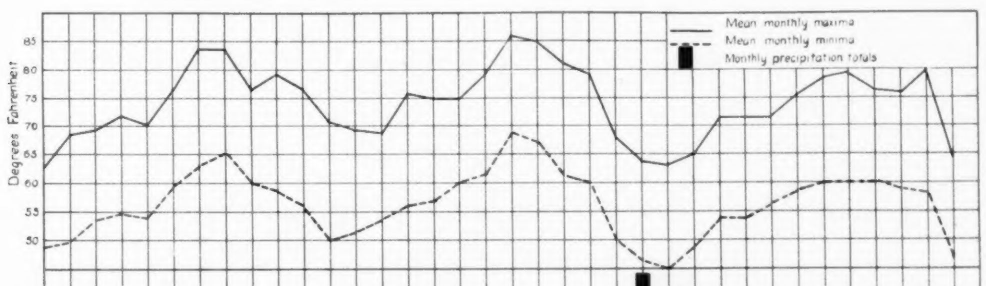

FIG. 3. Temperature and precipitation from January 1, 1930, to January 1, 1933. Weather Bureau, U. S. D. A., Los Angeles.

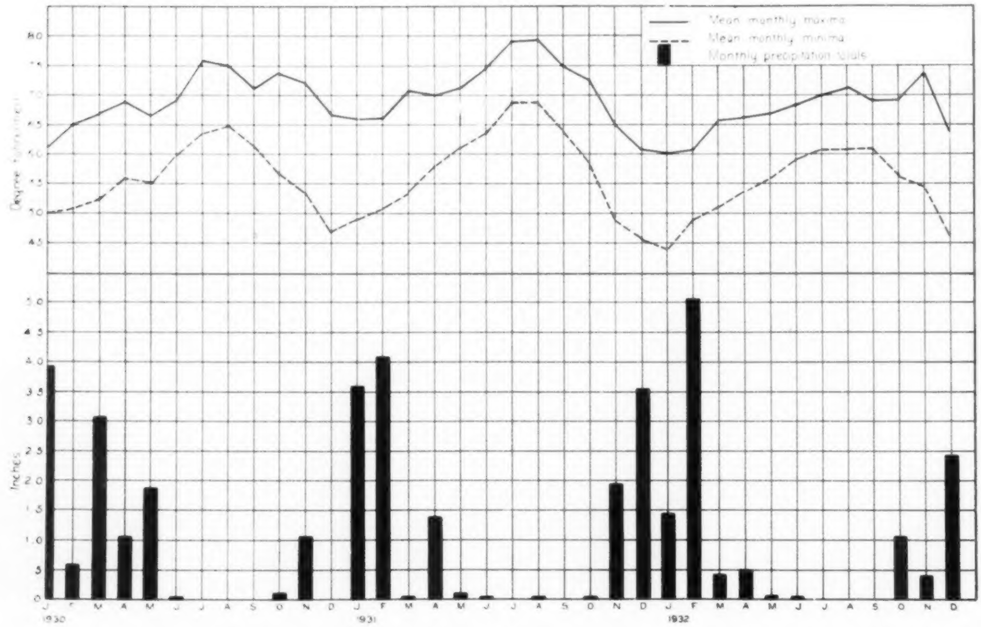

FIG. 4. Temperature and precipitation, from January 1, 1930, to January 1, 1933. Weather Bureau, U. S. D. A., San Diego.

between monthly means of the maxima and the minima was less throughout the year in San Diego than in Los Angeles, at the latter locality the summer mean maxima, for the three months July to September, being approximately 10 degrees greater than in San Diego. It would seem that in general the temperature is favorable for plant growth except when, at very infrequent intervals, it drops below the freezing point.

LIGHT

Maritime dunes are areas of high light intensity for the major portion of a year. In the two areas of investigation the air is clear with no noticeable smoke or soot, the light intensity being diminished, therefore, only by occasional foggy and cloudy weather. The number of days of dense fog, of cloudy and of partly cloudy weather, per month, from January, 1930 to January, 1933, obtained from the records of the Weather Bureau, U. S. D. A., at Los Angeles and San Diego, is given in Table 2. Dense fog occurs infrequently at either station, many months showing a record of but one such day. In San Diego, however, during this three-year period, fog was more frequent during February, October and November. The greater prevalence of fog in San Diego County renders the light over a period of a year less intense than at Los Angeles. Cloudy and partly cloudy days occur more often, appearing at irregular periods in each area.

To obtain a comparison of the radiant energy at some of the dune stations, Livingston black porous cup atmometers (1911) were operated for four

TABLE 2. Number of days of fog and of cloudy weather.[a]

Year and Month	Los Angeles County			San Diego County		
	Partly cloudy	Cloudy	Dense fog	Partly cloudy	Cloudy	Dense fog
1930 January	9	13	0	7	19	0
February	6	3	4	13	7	3
March	10	8	0	8	12	1
April	15	3	1	16	7	0
May	6	6	0	9	10	2
June	8	5	0	7	10	0
July	8	2	0	13	3	0
August	10	1	0	12	6	2
September	14	3	0	17	4	0
October	5	1	1	5	5	4
November	3	4	0	5	4	2
December	5	1	0	5	4	3
1931 January	5	8	0	11	7	1
February	8	8	0	10	10	0
March	9	3	1	6	6	1
April	8	9	0	11	10	0
May	17	4	1	16	6	1
June	14	3	0	9	6	1
July	5	1	1	17	3	1
August	8	3	1	9	6	0
September	5	3	0	8	3	0
October	5	8	1	13	3	1
November	7	7	1	8	9	1
December	10	9	1	10	11	0
1932 January	11	4	0	8	8	0
February	6	11	0	7	13	2
March	7	4	0	10	5	1
April	9	2	1	13	7	1
May	9	8	1	11	10	0
June	6	5	1	16	4	1
July	13	0	0	17	4	0
August	12	2	1	12	8	1
September	17	2	0	19	4	0
October	11	4	1	11	9	6
November	7	2	1	6	6	3
December	7	5	0	6	8	0

[a] Data from Weather Bureau, U.S.D.A., Los Angeles and San Diego.

months, from September, 1932 to January, 1933, this including the major part of the dry period immediately preceding the rainy season. Two of the atmometers were of the old type, the rest of the new type (Livingston, 1931). They were set up in the El Segundo area at the Ericameria station (3) and the Rhus station (4), and in the San Diego area at the Abronia station (5) and the Rhus station (6) of the Silver Strand. Readings of both the black and the white atmometers were taken weekly during this period (Figs. 5 and 6). A comparison of these data shows that the greatest radiant energy was at the Abronia station (5) on the Silver Strand, while the radiant energy at the other three stations, the Ericameria and Rhus at El Segundo and the Rhus on the Silver Strand, differs but slightly. For the most part, the rates from the white cups at the Abronia and Ericameria stations are higher than those from

the black cups at the two Rhus stations, indicating that the influences affecting evaporation measured by the white cups at the Abronia and Ericameria stations cause greater evaporation than do these same influences, to which is added that of light, measured by the black cups at the Rhus station. This coincides with the fact that Abronia as a pioneer exists under xeric conditions, Ericameria, farther along in the succession, exists under less xeric conditions, and that Rhus represents one of the later stages in the succession when conditions have proceeded farther toward mesophytism.

Most sand dune areas are characterized by exposure to light of high intensity. This is especially the case along the strand and in the moving dunes. Besides illumination from above, there must also be taken into account reflected and diffused light. The light-colored sand, which characterizes the dunes because of the generally sparse vegetation, greatly promotes light-diffusion. The reflection of light by the water and by the foam-crested

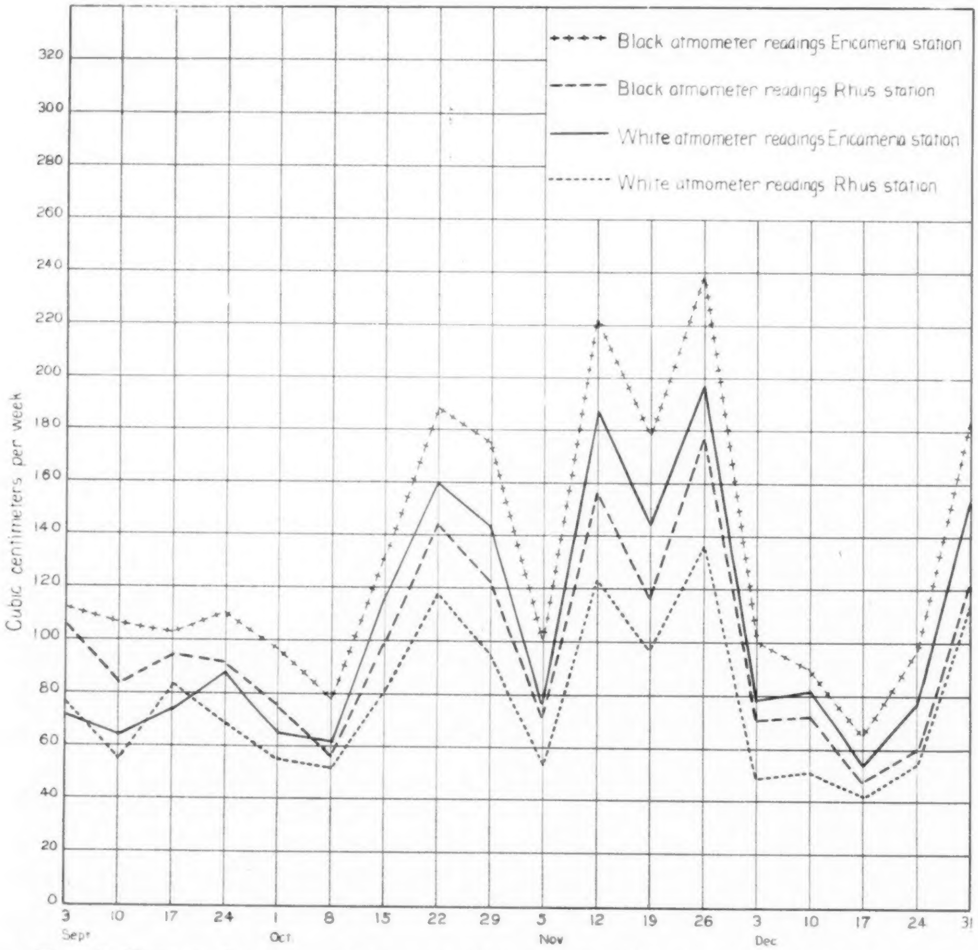

FIG. 5. Evaporation from black and white atmometers at two stations, Ericameria (3), and Rhus (4), El Segundo, Los Angeles County, September, 1932 to January, 1933.

breakers is an additional factor, especially at the Abronia station. Slopes facing south are more xeric than those facing north, this being due, not to the wind which in general is from the west, but to the sun and the resulting higher temperature.

WIND

The prevailing wind at San Diego is from the west, with an average velocity of 5.3 miles per hour for 1930, 6.6 for 1931 and 6.5 for 1932.[7] At Los Angeles the prevailing wind for most of the year is from the southwest, the average velocity being 4.5 miles per hour in 1930, 5.9 in 1931, and 5.8 in 1932.[8] The wind attains a velocity of twenty-eight to thirty miles per hour at times, this being sufficient to blow salt spray inland for a considerable distance. Sandblast, caused by wind-carried sand, carves living twigs (Cowles, 1899) as shown by Rhus in San Diego County. It is a probable cause in the limitation of the height of shrubs, as observed in Rhus on the Silver Strand. Thickets of Rhus in that location were found, too, to be partially dead on the side exposed to strong winds.

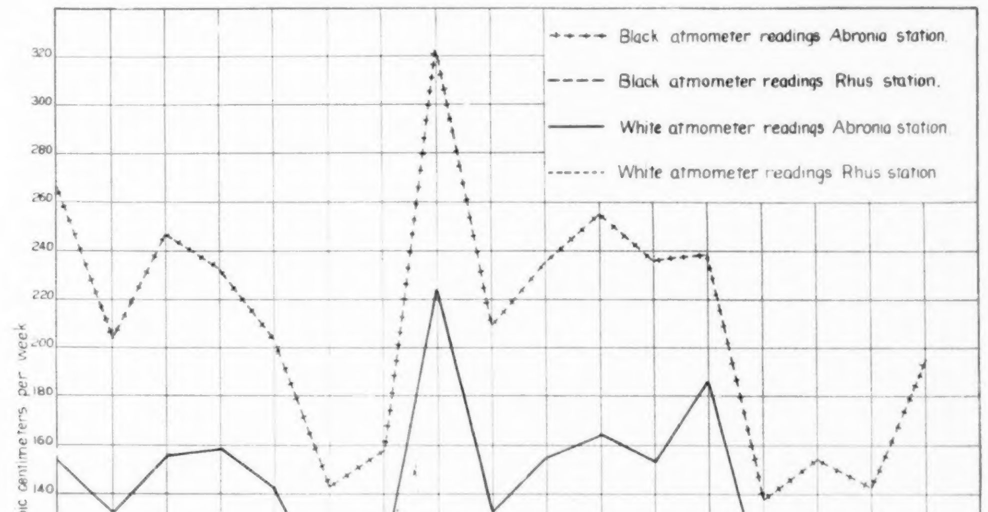

FIG. 6. Evaporation from black and white atmometers at two stations, Abronia (5), and Rhus (6), Silver Strand, San Diego County, September, 1932 to January, 1933.

[7] Weather Bureau, U. S. D. A., San Diego. [8] Weather Bureau, U. S. D. A., Los Angeles.

PRECIPITATION

Precipitation records[9] for San Diego and Los Angeles show a fairly close correlation. About ninety per cent occurs from the beginning of November to the end of April.

PRECIPITATION IN INCHES

SAN DIEGO

Year	Month	Monthly Maximum	Total for Year
1930	Jan.	3.90	11.73
1931	Feb.	4.11	15.16
1932	Feb.	5.15	11.34

LOS ANGELES

Year	Month	Monthly Maximum	Total for Year
1930	Jan.	5.57	13.02
1931	Dec.	5.95	18.93
1932	Feb.	5.33	10.72

Figs. 3 and 4 give the total monthly precipitation for three years, from January, 1930 to January, 1933. Comparison of temperature graphs with charts of total monthly precipitation at each locality shows that the period of the maximum precipitation does not coincide with that of maximum temperature; rain comes at the season which is most unsuitable for growth, the cold part of the year, and when the temperatures again become favorable for growth there is little or no precipitation.

Precipitation, while of interest for a comparison of various dissimilar dune areas, is approximately the same at the six stations established in the two dune areas investigated as appears to be indicated by the San Diego and Los Angeles records of the Weather Bureau. Therefore precipitation itself probably has but little differentiating effect on the plant life at the several stations.

While much of the rain quickly percolates to the water table and becomes unavailable to plants whose roots are in the upper layers of the sand, these plants may, nevertheless, obtain some moisture from that condensed on the surface of the sand. This condensation is due to rapid lowering of the temperature of the soil near the surface on summer nights.

If the supply of sand and the wind velocity may be considered as constant factors, the duration of the dry periods of the year may be said to govern the magnitude of a dune area. On the southern California littoral sunshine plays a large part in sand drying, sand being transported on all but a very few days of the year. The most favorable seasons for dune formation, however, are summer and autumn, especially that period just preceding the rainy season. In 1930, 1931, and 1932, the wind velocity averaged 4.9 miles per hour during August and September at Los Angeles and 6.2 miles per hour at San Diego. Some further facility is afforded then to sand transportation by wind, because, with the shortage of water, there is almost a cessation of

[9] Weather Bureau, U. S. D. A., Los Angeles and San Diego.

growth of sand-binding species, and this stabilizing element is then temporarily lessened.

HUMIDITY

The manner in which information on relative humidity is recorded at the Federal Weather Bureau stations is such that no satisfactory conclusions could be drawn from that source. The investigation of humidity, therefore, rests upon information obtained by means of a cog psychrometer at two stations established at the sand dunes, Abronia (5) and Rhus (6), on the Silver Strand. Weekly records were secured at approximately the same time of day over a period of four months, from September, 1932 to January, 1933. This interval included dry weather, which was broken in December by the advent of the winter rains. During these four months the percentage of relative humidity did not drop below fifty and on one day attained one hundred per cent. (See Table 3.)

TABLE 3. Relative Humidities at the Abronia and Rhus Stations (Silver Strand) between 3:30 and 4:30 P.M.

1932	Abronia station			Rhus station		
Date	Dry bulb Fahrenheit	Wet bulb Fahrenheit	Relative humidity %	Dry bulb Fahrenheit	Wet bulb Fahrenheit	Relative humidity %
September 27	65	58	66	64	58	70
October 4	67	59	62	67	58	58
11	63	58	74	66	61	75
18	64	57	65	65	58	66
25	68	59	58	69	60	59
November 1	64	60	79	67	64	85
8	69	59	55	68	58	54
15	62	59	84	64	59	79
22	60	58	89	60	58	89
29	62	58	79	61	59	89
December 6	60	56	78	59	56	83
13	51	51	100	51	51	100
20	61	56	73	60	55	73
27	63	58	74	62	56	69

SOIL CHARACTER

Soil samples collected at each station at depths of 25, 45, and 75 centimeters, were sent for analysis to the Bureau of Chemistry and Soils, U. S. D. A., Washington, D. C.

The samples, except that taken from the bluff, represent loose, incoherent sands, and range from rather coarse to medium grades. The component of highest percentage is quartz, ranging as high as ninety per cent, with a little feldspar and considerable basaltic material. Minute fragments of shells were found in some of the samples. The coarsest sands were at the Abronia while the finest were at the two Rhus stations. Dune soils are poor in nutrient materials; organic substances which may be left in the soil are rapidly de-

composed, and, owing to the physical structure of sand, rain water carries humus particles deep into the soil. This general type of soil is very permeable to water, since the soil particles possess little cohesion because of the porous structure of sand and its deficiency in colloidal material. There is usually a rapid drying of the surface after rains, the thin dry top layer probably conserving the soil moisture. In light rains, water may be evaporated from the surface before it can be absorbed by the soil.

SOIL MOISTURE

Determinations of water-content were made monthly at the Silver Strand, San Diego County, at the Abronia (5) and Rhus (6) stations from May, 1932 to February, 1933. Samples were taken at 10, 20, 30, 40 and 60 cm. A spade was used and the samples collected in numbered and weighed bottles. Each soil sample was obtained by pushing the mouth of the bottle into freshly exposed sand, and immediately thereafter the bottle was tightly stoppered. The first weighings were made within an hour after securing the soils and were carried out to thousandths of a gram. The sands were then dried in their open containers for forty-eight hours at a temperature ranging from 103 to 107 degrees Centigrade. The percentages of water were computed upon a dry weight basis, using:

$$\frac{\text{wet weight - dry weight}}{\text{dry weight}} \text{ X } 100 = \text{percentage of soil moisture.}$$

Table 4 and Table 5 give the percentages from May, 1932 to February, 1933, of the Abronia and the Rhus stations, respectively. This interval includes the critical period of the year, when there is but little moisture in the soil, and the period of rains of early winter.

During the rainy season there is an abundance of soil moisture except at the surface, which dries soon after a rain. During spring and early summer the water content decreases steadily; later in the summer, and until the early winter rains set in, the amount of water available is so slight that it is probable the plants suffer from a water deficit. As Cooper (1922) found in the case of a chaparral area, so also in these dunes in the present investigation a lag in the response of the lower layers of the sand to the first rains was noted, which shows that the advent of precipitation does not close the dry season in such layers of the sand as are occupied by the deep roots of Lupinus and Ericameria. Somewhat, too, as stated by Cooper for chaparral, there are three causes for the depletion of water in the dune soils. These are drainage of gravity water, evaporation from the surface of the sand, and water removal by plants. Shortly after the end of the rains the gravity water is removed from the upper layer of soil, while evaporation from the surface

TABLE 4. Percentage of moisture in soil at Abronia station (5).

Date	Depth cm.	Wet weight gms.	Dry weight gms.	Percentage of moisture
1932 May	10	109.62	109.07	.49
"	20	84.79	84.03	.90
"	40	72.81	71.48	1.80
June	10	105.45	104.90	.51
"	20	104.39	103.79	.57
"	30	85.30	84.19	1.30
"	40	96.94	95.60	1.40
"	60	91.62	90.08	1.70
July	10	83.38	82.97	.49
"	30	103.80	102.60	1.30
"	60	101.70	99.90	1.80
August	10	112.97	112.33	.56
"	20	110.92	110.31	.55
"	30	110.15	108.75	1.30
"	40	104.02	102.40	1.50
"	60	61.39	60.22	1.80
September	10	110.31	109.75	.51
"	20	101.71	101.16	.54
"	30	105.13	104.39	.71
"	40	100.07	98.32	1.70
"	60	104.59	103.18	1.30
October	10	107.19	106.93	.25
"	20	106.20	107.40	.74
"	30	102.94	102.35	.58
"	40	107.44	106.70	.69
"	60	106.99	106.27	.68
November	10	107.54	105.73	1.70
"	20	102.81	100.47	2.33
"	30	98.59	96.01	2.69
"	40	109.21	106.16	2.88
"	60	106.48	105.12	1.39
December	10	105.44	104.84	.57
"	20	101.35	99.52	1.84
"	30	101.71	98.77	2.97
"	40	101.92	99.07	2.88
"	60	101.79	98.59	3.24
1933 January	10	195.02	194.06	.87
"	20	196.60	195.74	.75
"	30	198.41	196.97	1.26
"	40	191.86	191.04	.74
"	60	193.18	191.56	1.48

continues for a longer period. Removal by plants continues during the year, or until such time as all available water has been removed.

SOIL TEMPERATURE

For determinations ordinary Centigrade chemical thermometers and maximum and minimum thermometers were used. When taking soil samples, chemical thermometers were inserted in the freshly exposed sand at different depths at the Abronia (5) and Rhus (6) stations on the Silver Strand. Surface temperatures were also taken in sun and shade, the bulb of the thermometer being thrust into the sand just below the surface. These data were

TABLE 5. Percentage of moisture in soil at Rhus station (6).

Date	Depth cm.	Wet weight gms.	Dry weight gms.	Percentage of moisture
1932 May	10	106.00	105.39	.58
"	20	100.67	98.06	.26
"	40	101.62	98.78	.28
June	10	99.47	98.83	.65
"	20	100.01	99.24	.77
"	40	92.16	90.42	1.80
"	60	95.33	93.91	2.50
July[10]	..	......	......	....
August	10	103.94	103.43	.49
"	20	107.63	106.98	.60
"	30	102.27	101.60	.65
"	40	83.00	82.02	1.00
"	60	82.60	81.70	1.10
September	10	107.20	106.72	.44
"	20	104.39	103.79	.57
"	30	103.95	103.29	.62
"	40	103.14	102.22	.89
"	60	99.32	98.52	.81
October	10	100.29	98.90	1.40
"	20	97.79	94.10	3.90
"	30	100.26	97.64	2.60
"	40	94.26	92.48	1.10
"	60	97.56	96.81	.78
November	10	97.45	94.92	2.66
"	20	92.43	89.59	3.15
"	30	93.92	90.64	3.67
"	40	84.26	80.35	4.86
"	60	97.55	94.61	3.10
December	10	97.89	95.83	2.15
"	20	100.93	97.76	3.25
"	30	100.00	97.07	3.02
"	40	96.54	93.11	3.69
"	60	98.44	94.96	3.67
1933 January	10	181.59	175.54	6.53
"	20	180.97	178.90	2.13
"	30	179.13	171.54	8.44
"	40	174.88	166.97	9.31
"	60	189.58	185.66	3.81

[10] Data lacking for this month.

obtained from June, 1932 to January, 1933, and in the case of the Rhus station some additional data became available for March, April and May. All these are given in Tables 6 and 7.

Following approximately the methods of Toumey and Stickel, 1925, maximum and minimum thermometers were placed horizontally at a depth of 45 cm. in wooden boxes constructed so as to prevent circulation of air while at the same time permitting ready access to the instruments. This installation was made at five stations, namely, El Segundo, moving dune station (2), Ericameria (3), and Rhus (4), and at the Silver Strand, Abronia station (5) and Rhus (6). Readings were taken weekly from September, 1932 to January, 1933 (Table 8).

TABLE 6. Soil temperatures at Rhus station, Silver Strand.

Depth cm.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
	Degrees Centigrade									
Surface in sun	....	..	37	35	37	42[11]	36	32	25	cloudy
Surface in shade	25	28	30	31	32	30	30	24	22	20
10	22	25	26	32	32	30	27	20	20	18
20	19	20	21	28	29	25.5	25	19	18.5	18
30	18.5	19	20	25	25	25	24	19	18	17
40	....	..	..	24	24	25	23	20	18	17
60	....	..	..	23	24	24	22	20	18	17

TABLE 7. Soil temperatures at Abronia station, Silver Strand.

Depth cm.	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
	Degrees Centigrade						
Surface in sun	36	38	43[11]	37	33	23	cloudy
Surface in shade	29.5	30	30	29	25	18	18
10	31	31	27	25	19	20	18
20	27	27	26	23.5	18.5	18	17.5
30	26	25	24	22	19	18	17.5
40	24	23	23	22	19	18	17.5
60	22.5	22	22	21	20	19	17.5

[11] Temperatures taken in August in forenoon instead of afternoon.

The maxima at the five stations show considerable uniformity, the moving dunes exhibiting the greatest differences. For the week ending December 3, 1932, the maximum temperature at the moving dune station at El Segundo was seventy-four degrees Fahrenheit, ten degrees higher than at the Abronia and Rhus stations on the Silver Strand and nine degrees higher than the Ericameria and Rhus stations at El Segundo, the smallest differences occurring at the Rhus stations. The minima show more uniformity on the whole, with the exception that during this period of four months, the lowest minimum recorded, for the week ending December 17, 1932 at the El Segundo moving dune station, was eleven degrees less than at the Abronia station, Silver Strand, for the same period. By comparison of maxima and minima at any one station it becomes evident that the temperature range from week to week is small, usually four to eight degrees, running higher at the Abronia station, while at the moving dune station on two occasions the weekly range was fourteen degrees. Throughout these four months in which the lowest temperature, forty-five degrees, was reached but once, in December, there was no time during which low temperature could have affected metabolic processes seriously or prevented root growth.

Soil temperatures at the surface and at about ten centimeters depth are not only higher at times but are also subject to greater fluctuation than those at greater depths. Thus roots which are close to the surface, are subject to

TABLE 8. Weekly maximum and minimum temperatures.

Date	Abronia Silver Strand		Moving dunes El Segundo		Ericameria El Segundo		Rhus Silver Strand		Rhus El Segundo	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
	Degrees Fahrenheit									
September 3.......	80	73	82	72	76	70	74	71	74	69
" 10.......	79	72	80	72	76	71	74	69	72	69
" 17.......	78	70	74	68	74	70	71	69	71	68
" 24.......	76	70	75	72	71	70	70	69	72	69
October 1.......	76	68	77	67	72	66	70	68	75	67
" 8.......	74	67	75	67	74	66	71	66	73	66
" 15.......	73	65	74	64	73	65	67	65	69	65
" 22.......	68	59	75	61	71	63	69	60	68	60
" 29.......	70	60	74	67	67	63	67	64	65	61
November 5.......	68	60	74	65	67	61	66	62	64	60
" 12.......	71	59	74	66	66	62	66	62	69	60
" 19.......	68	59	73	65	65	61	66	63	63	59
" 26.......	66	60	73	62	67	60	65	62	65	58
December 3.......	64	57	74	63	65	58	64	59	65	56
" 10.......	68	56	69	62	63	56	62	53	65	51
" 17.......	68	56	59	45	57	48	58	52	61	47
" 24.......	58	52	61	52	57	48	62	52	59	47
" 31.......	58	52	62	49	55	50	59	52	56	51

the influence of an environment which is quite different from that affecting roots growing at deeper soil levels.

BIOTIC FACTORS

Biotic factors do not exert a marked influence in the sand dune habitat. This, in itself, constitutes an important feature, being responsible for much of the distinctive character of the vegetation. No earthworms, which play so beneficial a rôle in certain other soils, are to be found here. Where the vegetative cover has become established small accumulations of humus may occur, and during the rainy season mushrooms are found growing here and there. A rather important influence is that of the fires which occasionally run through the later stages of the plant succession.

AUTECOLOGY OF ELEVEN SAND DUNE SPECIES

THE SPECIES

Floristically considered, the coastal sand dunes of southern California contain a large number of annual plants, over 50 species being represented in San Diego County. The study of these, however, has been limited in the present work to their identification, since they are of little importance in succession, tiding over the long unfavorable period in the form of seeds. All of

the species investigated are perennials, existing under adverse conditions for the greater portion of the year over a number of years, and showing more or less modification for their environment.

Out of the large number of perennials inhabiting these coastal dunes, certain species were selected which are preëminent because of their positions in the succession, their distribution, and their adaptation to the environment, as attested by their abundance and successful maintenance.

METHOD OF INVESTIGATION

Field studies were made of the coastal dunes from Florence, Oregon, to Ensenada, Baja California. In these the locations of each of the chosen species on the strand, the moving dunes, and the stabilized areas, were noted. Each species was investigated as to its range, its actions as pioneer or invader, and its ability to endure covering by sand. At least ten examples of each species were examined, the size, gross morphology, type of branching, rate of growth, time of flowering, depth of roots, and types of roots being noted.

Measurements of the entire plant were made in the field. For the root system the surface sand about the plant was removed. Pieces of lumber, 4 by ⅞ inches, by 8 feet, were driven into the sand and then nailed together to prevent a cave-in. The distance from the plant at which this structure should be constructed was carefully estimated to prevent the planks from interfering with a root or being forced upon it, thereby breaking or injuring it. Photographs of the plant were taken during the process of excavation.

Measurements of the root systems were made as follows: after some of the surface sand had been removed, enabling a rough location of the more important roots, the general extension and the directions of the parts of the root system were carefully noted. The whole area estimated to be occupied by roots was then crossed by tapes firmly attached to stakes, marking off one-foot squares. The actual locations of the roots were obtained by careful digging with trowel and hands. For recording the horizontal locations a paper divided into one-inch squares was used. Each square inch representing one square foot of ground was subdivided into 100 smaller squares. For recording vertical distribution the horizontal record was made use of in connection with a vertical projection of the root system, depths being obtained by measurement. For representing the aerial portions of the plant, measurements were taken before excavation of the root system was begun. The vertical drawing includes shoot as well as root system, the horizontal drawing the lay-out of the root system only. In the vertical drawings, the root systems which come in a nearly vertical plane are shown, those at right angles being indicated by a dot when they diverged from the vertical. The horizontal plan represents the entire root-system as seen from above. If, for any reason, roots were not followed to their termination, the diagram indicates this by a

broken line. Weaver's (1927) methods were followed as closely as possible. Later, when the plant was excavated, in order to verify the measurements, the entire root system and the aerial portions as well were remeasured.

For minute characteristics, material collected in both areas was used. In order to obtain a representative size, mature leaves were measured over a period of a year in order to include both the dry and rainy seasons. From 50 to 200 specimens of each species were employed for this purpose.

Leaves, herbaceous and ligneous stems, and roots were sectioned in the investigation of the minute anatomy. The leaves and stems were gathered from the upper portions of vigorous plants, that were fully exposed to the prevailing environmental conditions. Slides were made of fresh material as well as of material embedded in paraffin and celloidin. For killing plant material formal-acetic alcohol was employed. Various stains were tried—light green, gentian violet, fuschin, safranin, orange G, and Bismarck brown. Microtome sections from ten to twenty microns in thickness were cut, the thickness depending upon the character of the material.

Tests for mucilage, resin, oil, cutin, and certain other substances, were made on fresh material.

When the count of the stomata was difficult to obtain, the epidermis was covered with a commercial collodion preparation. After drying, this collodion film was peeled off, and from it stomatal counts were made.

ABRONIA MARITIMA NUTT.

HABITAT

Abronia maritima grows upon the first or foredunes, the embryonic dunes which rise from the uppermost part of the strand. It may, however, extend its prostrate branches upon the very surface of the strand, where possibly winter's highest storm waves may reach them. At that season of the year the waves frequently lash at these dunes, exposing the roots of Abronia and often undermining small dunes. *Abronia maritima* is associated with few plants on the strand. Occasionally it may be found growing with Franseria and Atriplex.

This Abronia, because of its activities, is the principal pioneer, beginning its development in fresh-blown sand. The species, however, may be found also in locations a considerable distance from the ocean where the older, longer stabilized vegetation has not succeeded in holding the sand and movement has begun. For this reason there does not seem to be any correlation between *Abronia maritima* and proximity to salt water or salt spray. Fungi are frequently found growing in small mounds of Abronia where humus has collected.

AERIAL PARTS

The stems of *Abronia maritima* are prostrate, forming a mat that in some cases may reach a size of fifty by twenty-five feet. When sand collects around the plant an upright position is maintained by the support thereby afforded. When sand ceases to collect about the plant the branches, being too heavy to stand upright, fall to the surface of the sand with just the tips abruptly extending upward, making the plant at most about eight inches in height. From the center a large number of branches extend in all directions, forming a mat of vegetation which aids in the fixing of the sand and in the formation of a dune.

The stems and leaves are stout and fleshy, the usually unequal leaves of a pair being vertical in position, broadly ovate to oblong, round at the base, obtuse, irregularly slightly undulate, and with stout petioles. The average[12] length of leaf (blade with petiole) is 4.0 cm.; without the petiole, 3.0 cm. The width is 2.0 cm.; thickness, 2.9 mm. Fleshy leaves of plants on the strand at the sand dunes near Guadalupe averaged 5.5 mm. in thickness.

Buds form at all seasons, but are most abundantly produced in spring.

SUBTERRANEAN PARTS

The root system consists of a tap root with a few secondaries, the roots being strong and tough, but not extensive (Pl. 1). The system as a whole, has very few absorptive roots as compared with those of some of the other species considered. The maximum depth attained, unless covered by drifting sand, is about two feet. Two or three feet of spread from the tap-root may be expected, but aerial stems, buried in the soil, may aid in spreading the plant farther. Although the tap-root may be thick at its juncture with the stem, it tapers rapidly and comes to an abrupt end. In some of the excavations on the strand, the tips of the roots were found to be dead several inches above the level of the salt water. Sand collected from just below the ends of such roots showed a slight saline reaction.

ANATOMY OF THE STEM

The major tissue of the stem is water accumulative, mechanical tissue being small in extent. In the epidermal layer, averaging 0.025 mm. in width, with its many well-developed, multicellular, glandular trichomes, are occasional, slightly sunken stomata. The epidermis is covered by cuticle,[13] 0.002 mm. thick. Solereder (1908) states that the deposition of crystalline granules, consisting of calcium oxalate, occurs in the cell-walls of the epidermis of stem and leaf in Abronia.

Below the epidermis there is a layer of chlorenchyma as wide as the epidermis. Inside of the chlorenchyma, water accumulative tissue occurs,

[12] Throughout this paper, unless otherwise stated, an average for each species was obtained from at least fifty specimens, but for the most part one hundred were used.

[13] The use of the term "cuticle" in this paper is that given by Eames and MacDaniels, 1925

composing from one to two-thirds of the diameter of the stem. This tissue is composed of cells three to six times the thickness of the epidermal cells. Bundles of raphides consisting of long acicular crystals of calcium oxalate are present here (Pl. 2).

Concerning the stems of the Nyctagineae, Solereder (1908) says:

> The anomaly consists in the appearance, in the pericycle, of successive rings or strips of cambium, which produce secondary collateral vascular bundles, and conjunctive tissue on their inner side. The prosenchymatous conjunctive tissue bears simple pits like the wood-prosenchyma of the vascular bundles, from which it is difficult to distinguish, and is sometimes traversed by typical medullary rays.

Within the secondary vascular bundles are the primary, with pith parenchyma occupying the center of the stem, the pith being well developed.

Anatomy of the Leaf

The most noticeable feature of the leaf is the large amount of water accumulative tissue, extending throughout the leaf between the epidermal surfaces. The epidermis averages 0.04 mm. in width, being about equally thick on both sides. Leaves from a prostrate stem usually assume a vertical position which affords equal lighting on the two sides. Both epidermal surfaces bear about the same number of closely placed, uniseriate, multicellular, glandular trichomes, in length about five times the diameter of the epidermis. These trichomes have spherical heads, which are larger than the cells of the stalk. The petioles are also covered with glandular trichomes.

The stomata, on both surfaces, are somewhat sunken and are surrounded by glandular trichomes. The stomatal count[14] averages twenty-one per square millimeter on the adaxial surface and twenty on the abaxial. The cuticle is about 0.005 mm. thick on either surface.

The leaf is of the diplophyll type bearing chlorenchymatous cells, many of them enlarged and containing water, and frequently about six times the diameter of the epidermis in length. Chloroplasts are very numerous, scattered throughout the cells, and average 2.80 to 3.15 microns in diameter. They appear to be smaller toward the center of the leaf, and are found even in the water tissue around the veins. The intercellular space system is scanty. The cells of the water tissue were turgid at all times when examined, except that during the rainy season they seemed to be slightly less turgid than during the dry season. Bundles of raphides of calcium oxalate occur in the water accumulative tissue.

Measurements of the thickness varied considerably, depending upon the location in which the specimens were gathered. The average thickness of 2.9 mm. is exclusive of the trichomes, these increasing the thickness by 0.4 to 0.6 mm. Leaves of plants near the ocean were thicker than those collected inland.

[14] Pieces of epidermis were stripped from the periphery and from near the midrib because of variation in the number per unit of area. In all cases at least ten specimens were used.

ANATOMY OF THE ROOT

The roots of *Abronia maritima* do not show any special adaptations. The older roots and those near the surface or exposed to the air, are covered with a layer of bark. In younger roots a layer of cork surrounds the cortex, which is composed of large parenchyma cells. The anomalous structure of the roots corresponds with that of the stems, in that there is a concentric arrangement of secondary vascular bundles and of parenchyma formed within the pericycle. The xylem of the vascular bundles has large tracheae. In the pith parenchyma is a ring of these bundles occupying the center of the root.

SUMMARY

While *Abronia maritima* does not have an extensive root system, the character of some of its aerial parts tends to cut down the water loss and to hold water for use during unfavorable periods. Since the species is a prostrate plant, the desiccating effect of winds is largely avoided. The approximately vertical position of the leaves permits the rays of the sun to strike them at an angle, whereby transpiration is probably reduced and less reflected light from the sand received.

Some modifications are: diplophyll type of leaf, with most of the leaf converted into water accumulative tissue; presence of trichomes on both surfaces of the blades, and on the petioles and stems; cuticle; few stomata per square millimeter; stomata slightly sunken: death of some of the leaves during drought, some of them remaining on the plant and affording some protection from wind and sun.

Since this species is usually on or near the strand, its root system could not extend to a great depth without reaching salt water. To aid the organism in tiding over the rainless season, the plant depends not only upon water absorbed by the roots but also upon water in the form of dew or fog absorbed by the leaves.

Growth is apparently not influenced by the salt spray deposited upon plants growing near the strand, since such specimens are as healthy as those in open areas removed from the strand.

CONVOLVULUS SOLDANELLA L.

HABITAT

Convolvulus is found on sandy sea beaches, growing on the strand and in open places in the dunes. It is not usually associated with other plants, but is found in flat areas between hummocks overgrown by *Abronia maritima* and Franseria, and has not been found in habitats other than sand dunes.

AERIAL PARTS

This species has a prostrate growth habit, with its subterranean portion more extensive than observations of the aerial parts would indicate. The rhizomes grow about 4 to 6 inches below the ground surface, one specimen, only partly excavated, extending 55 feet and bearing numerous branches. From the alternate nodes of a rhizome there arise short upright stems with small clusters of from four to six foliage leaves (Pl. 3). In spring the stem may rise to the surface, form a small arch and return to its level in the soil, or it may continue its growth for several feet along the surface.

The thick, succulent leaves are reniform and of a deep green color, the adaxial surface glabrous and shining. The average length of a leaf (blade and petiole) is about 5.0 cm., the length and the width of the blade 1.8 cm. and 4.0 cm., respectively, and the thickness 0.50 mm. The petioles are stout, white to red in color, with considerable variation in length. The branch tips bear three to six turgid green leaves, while those farther from the tips soon become yellow and flaccid.

SUBTERRANEAN PARTS

The rhizomes of Convolvulus are succulent, pink to tan, varying from 25 to 50 feet in length. Short roots about 6 inches in length, develop from the underground stem at the nodes, the absorptive system being thus very meager.

ANATOMY OF THE STEM

The most noticeable internal feature of the stem is the large amount of succulent tissue. The entire stem is composed of this with the exception of the vascular tissue and epidermis. A transverse section of the aerial stem presents a somewhat irregular outline. The epidermis, 0.025 mm. thick, has but few stomata and is covered with cuticle of about 0.002 mm. thickness. On the inner side of the epidermis the cells of water accumulative tissue gradually increase in size toward the center. Anthocyanin is present within the cells just below the epidermis, but no chloroplasts were found. The vascular system is of the dictyostele type composed of bicollateral bundles with but little development of tracheae and tracheids. Of the stems that were examined, the pith occupies less than one-third of the diameter.

The underground stem is about two to three times the diameter of the aerial stem and is of similar structure. No stomata or chloroplasts were found in the rhizomes.

Non-anastomosing laticiferous vessels are found in the cortical and in the pith parenchyma of both the aerial stem and the rhizome, being especially abundant in the latter (Pl. 4).

ANATOMY OF THE LEAF

The leaf epidermis, about 0.03 mm. thick, with walls slightly thicker on the outside, is covered with a fairly heavy layer of cuticle, averaging 0.004 mm. on the adaxial surface and 0.003 mm. on the abaxial. The stomata, which appear in both surfaces, are but slightly sunken in the epidermis, and are accompanied by two subsidiary cells. There are about 155 stomata per square millimeter on the adaxial surface; 150 on the abaxial. The stomata average 0.035 mm. long and 0.040 mm. in width, including the subsidiary cells.

Below the adaxial surface are from three to six rows of palisade cells. Somewhat more than one-half of the mesophyll in the abaxial portion of the leaf is composed of compact spongy chlorenchyma. Small acicular crystals are found in the mesophyll, usually grouped into bundles of raphides. The latex occurs in large laticiferous ducts located on the adaxial side of the larger veins. There is little intercellular space except near the stomata on the abaxial surface, the palisade layers on the adaxial surface being particularly compact. The succulent appearance of the leaf is due to the large amount of water in the chlorenchymatous tissues.

ANATOMY OF THE ROOT

In a transverse section of younger roots small patches of collenchyma are seen. In older roots the development of phellogen results in a narrow layer of cork, within which the cortical parenchyma, composed of rather large cells, occupies about three-fourths of the diameter of the root, with a circle of multicellular laticiferous tubes at regular intervals. Starch grains were found to be abundant in the cells of the cortical parenchyma. The endodermis is well defined; the xylem of the stele consists of a few tracheae surrounded by wood fibers.

SUMMARY

The low habit of growth of Convolvulus off-sets the desiccating influences of the sand dune habitat. Its rhizomes are very succulent, due to the presence of a large proportion of water accumulative cells and latex vessels. The root system is meager as compared with that of the other ten species investigated. The epidermis which is covered with cuticle has numerous stomata in both surfaces of the leaves; stomata occur only sparingly on the aerial stems. The cells of all tissues are very closely placed, leaving but a small proportion of intercellular space.

ATRIPLEX LEUCOPHYLLA DIETR.

HABITAT

This perennial Atriplex generally forms small hummocks in the open areas of the strand. It grows rather close to the ocean, often associated with *Abronia maritima* and sometimes with Franseria.

Aerial Parts

The plant is reclining or, when sand accumulates around it, maintains itself in an upright position for not more than six inches above the surface. In all specimens excavated the stem branching began at 6 to 8 inches below the surface; with progressive burial the stems grow upward. The spread is about 2 to 3 feet from the crown of the tap root (Pl. 5).

Branches are numerous, alternate in arrangement, very short and stout, and somewhat woody at the base.

The pale green leaves are densely scurfy, thick, orbicular to elliptic, entire, sessile, three-nerved, acute, averaging 1.0 cm. in length, 7.0 mm. in width and 3.2 mm. thick at the mid-rib.

Subterranean Parts

The root system is fairly extensive as compared with the shoot system. In all the plants excavated it was found to consist of a tap-root extending 2 to 4 feet below the surface, its length depending upon the amount of burial by sand. Secondary roots coming from the tap-root extend at different levels as far out as the aerial parts extend.

Anatomy of the Stem

The epidermis, bearing stomata, is densely scurfy with overlapping trichomes. These are vesicular hairs, composed of one-celled scales and one to two-celled stalks. Scales are of two sizes, the larger about eight times as long as the width of the epidermis. The walls of the epidermal cells are of equal thickness on all sides, the cuticle being about 0.002 mm. thick. At the inner side of the epidermis there are two to three rows of collenchyma cells. The young stem develops a few groups of chlorophyll-bearing parenchyma cells slightly larger than those of the epidermis. The cells of the cortical parenchyma, in size about three times that of the epidermal cells, act as water accumulative tissue and contain large druses of calcium oxalate. The conducting system is a large polyarch dictyostele with collateral vascular bundles. The center of the stele is occupied by an extensive pith, whose cells contain druses. The tissues of the stem are compact, with little intercellular space, except near the occasional stomatal structures. Anthocyanin is present in the epidermal layer and in a few cell layers beneath it. As growth proceeds, the anomalous structure of the stem becomes evident in the development of secondary vascular bundles (Solereder, 1908).

Anatomy of the Leaf

The leaf is thickly covered on both surfaces with trichomes of vesicular hairs which are of two sizes, the larger two to three-celled, the smaller unicellular. The length of the larger is greater than the diameter of the leaf.

The epidermis, about 0.015 mm. thick, consists of a single layer of cells, whose walls are of equal thickness. Both the epidermal surfaces are covered with a thin layer of cuticle, about 0.0025 mm. thick on the upper surface and 0.0016 mm. on the lower. Slightly sunken stomata are present in both layers. The stomatal count for the adaxial surface was one hundred per square millimeter; for the abaxial one hundred and ten. The average length of a stoma is 0.023 mm. and its width 0.015 mm. Below the epidermis is a layer of water accumulative tissue in which are special cells bearing large druses of calcium oxalate. This leaf differs from all others of those investigated in that the palisade tissue does not appear directly below the epidermis but is located under one or more layers of water accumulative tissue. The veins are surrounded by a zone of chlorenchyma, the midrib, however, possesses only two lateral patches.

The tissues are compact, with few intercellular spaces, except in the immediate vicinity of the stomata.

Solereder (1908) referring to the Chenopodiaceae states that

> the most noteworthy features in the structure of the leaf are the absence of a definite type of stoma, and of typical spongy tissue, which has not been observed in any species. In spite of the xerophilous character of many species the cuticle rarely attains a considerable thickness, nor have mucilaginous epidermal cells been observed.

The leaf in cross section measures on the average 0.75 mm. including the trichomes, and 0.25 mm. without them; at the midrib it is about 0.91 mm. thick (Pl. 6).

ANATOMY OF THE ROOT

There is a thin layer of cork on the mature root beneath which there is cortical parenchyma composed of large, thin-walled cells. After secondary thickening has developed, the cortical parenchyma is present as a rather narrow zone. The anomalous structure of the root is seen in the formation of pericyclic rings or strips of cambium, which form concentric zones of vascular tissue and thin-walled parenchyma cells (Solereder, 1908).

SUMMARY

While Atriplex has frequent stomata per unit of area on both surfaces of the leaf and on the stem, excessive transpiration is probably checked by the scurfy surface and by over-lapping trichomes, which provide a dead air space above the epidermis. Transpiration is probably further retarded by the slightly sunken stomata, the closely placed cells, and the presence of cuticle. Water is retained in peripherally placed water accumulative tissue. The extensive xylem of the root system may serve to supply this plant advantageously with water when the soil moisture is ample. Light does not reach the chloroplasts readily, due to the trichomes and to the embedding of the chlo-

renchymatous tissue. This species appears to be able to withstand sand covering as it is usually found growing in a partly buried condition. It appears to thrive in unstable soil exposed to severe wind, where evaporation rates are high, heat intense, and direct and reflected light strong.

MESEMBRYANTHEMUM AEQUILATERALE HAW.

HABITAT

The character of the soil does not appear to be of great importance for this species, since it is found on sand and on sandy and clayey loams of coastal dunes and bluffs, making its best growth, however, on the sand dunes. It occurs in the foredunes behind the strand, and in rear portions of the dunes, either alone or associated with any of the species of the more stabilized areas. Since it is a sand-binder and dune-former, making its appearance usually after such a true pioneer as *Abronia maritima* and others of its sort, it may be classed as a secondary pioneer. Mesembryanthemum is often employed under cultivation as a sand-binder.

AERIAL PARTS

The species is a prostrate perennial herb, forming extensive mats, often fifteen to twenty feet in diameter. Much of the older portions of the plant dies during late summer and autumn, before the succeeding rainy season begins. Water is conserved by the younger branches until the rainy season commences, and the plant is thus carried over the critical period.

Young stems are fleshy, non-terete, and almost as great in diameter as the leaves. In age the stems shrink radially and become hard and brittle.

Succulence is due mainly to the fleshy leaves which are three-sided, opposite in pairs, without stipules, and mostly nearly vertical in position. Their nearly flat sides are smooth and somewhat less broad than the thickness of the leaf. A leaf averages about 5.0 cm. in length, 1.2 cm. in width on the wider face of the inequilateral triangle, and about 0.9 cm. wide on the other two faces.

SUBTERRANEAN PARTS

The fibrous root system is meager as compared with the size of the plant, completely lacking the extensive branching observed in many of the dune species. The roots are all superficial, and consequently efficient in absorbing the moisture from light rains and from condensation of water vapor of fogs and dew upon the soil, but the roots are unable, from their superficial character, to obtain water which is located much below the surface. Since the plant develops roots at the nodes as the stems grow extensively over the surface of the ground, sand-binding is a prominent feature. Many new roots develop after the beginning of the winter rains, but none becomes extensive either in length or diameter (Pl. 7).

Anatomy of the Stem

The young stems are very fleshy, and their epidermis bears stomata, but lacks trichomes; it is covered with a layer of cuticle, 0.005 mm. in thickness. On the inner side of the small epidermal cells, as seen in transverse section, are two to three rows of small round chlorenchymatous cells. The rest of the cortex is composed of cells which vary in size from about that of the epidermal cells to about six times their diameter. In these cortical cells, with their large percentage of water, giving the stem its succulence, are found occasional chloroplasts and many bundles of raphides; small vascular bundles are interspersed. A conspicuous endodermis surrounds the stele. In the center of the stem is the vascular tissue which appears somewhat oblong in cross-section. The cells of both the tracheids and tracheae are very small as compared with those in the succulent tissue, while the tracheae are small in number as well. The stem, in which no vascular rays are present, is anomalous in structure due to the peculiar arrangement of the concentric vascular areas (Solereder, 1908). In the center is the pith in which are occasionally deposited bundles of raphides. The younger stems of this species contrast strongly with those of the other plants investigated as regards their extreme succulence and small amount of mechanical tissue. The older stems, with only their conductive tissue in use, are brown and shriveled.

Anatomy of the Leaf

The triangular leaf has its epidermis,[15] which is 0.02 mm. thick, covered on all three sides of the leaf with a heavy layer of cuticle, about 0.004 mm. in thickness. Stomata on all three surfaces have an outer stomatal chamber formed by an overhang of the two subsidiary cells. The guard cells, small in size, are sunken to the inner side of the subsidiary cells; below them is located the inner stomatal chamber. There are on an average about 90 stomata per square millimeter on the adaxial surface of the leaf, and about 86 per square millimeter on the two abaxial surfaces. The length of the stomata averages about 0.04 mm. and the width, 0.03 mm., including the subsidiary cells.

For a comparison of stomatal counts, a Mesembryanthemum plant of the same species, probably an escape from cultivation, growing in a shaded location in a vacant lot in Los Angeles, was examined. Its stomata numbered 280 per square millimeter on the adaxial surface and 268 on the two abaxial surfaces, the size of the stoma also differing. On the adaxial surface of the leaf the length of the stoma averaged 0.01 mm. while on the abaxial surfaces, it was slightly more than 0.015 mm. in length and 0.005 mm. in width.

In the sand dune habitat the palisade tissue, directly under the epidermis on all three sides of the leaf, is composed of two to three rows of long and

[15] According to H. Solereder (1908), "in Mesembryanthemum it [calcium oxalate] also occurs in a deposition in the cell wall in the form of small crystalline granules, found principally in the outer wall of the epidermal cells of the leaf."

narrow cells with chloroplasts lining their walls. This tissue comprises but little of the total volume of the leaf. Sclereids are found at intervals in the palisade, and these mechanical cells extend from the epidermis to the succulent tissue. They are Y-shaped and closely placed in the palisade, which is very compact except at the stomatal openings. On the inner side of the palisade tissue the entire leaf, except for the vascular bundles, is composed of large-celled succulent tissue, many of these cells being ten times as long as those of the epidermis. Bundles of raphides, consisting of needle-shaped crystals of calcium oxalate, occur frequently in these. Among the palisade cells are long and wider cells containing mucilage, while in the succulent tissue there are very large, rounded and sometimes elongated, mucilage cells (Pl. 8).

The vascular system, as seen in cross-section, consists of small cells and is comprised of a principal bundle in the center of the leaf with smaller bundles in the succulent tissue; a parenchymatous sheath of small cells surrounds the principal bundle. A patch of sclerenchyma is located on the outside of the phloem.

Anatomy of the Root

The root contains underneath its epidermis large cells of cortical parenchyma, these acting possibly as water accumulative tissue, to judge from the succulence of the young root. In the cortical parenchyma bundles of raphides are occasionally present. The anomalous structure of the stem is repeated in the older root by its concentric rings of xylem and parenchyma (Solereder, 1908).

Summary

Since the root system is a shallow one, the plant must depend upon succulence to maintain it through the dry summer months. It is a common occurrence for the older parts to die, and this to so great an extent that only half a dozen of the green triangular leaves may remain at the end of each stem at the close of summer. This procedure is of great assistance in maintaining the plant during the critical period. Leaves were examined at all seasons of the year, and it was observed that during the dry period the leaves which remained green were as turgid as leaves on similar plants in the rainy period.

The position of the leaf is vertical, affording thus reduced exposure to direct rays of the sun. Being three-sided, the leaf has a small surface exposure in proportion to its volume. Protection from desiccating winds is afforded by the low position. Both young stems and leaves, consisting mainly of water accumulative tissue, are extremely succulent, there being but a small quantity of conductive and practically no mechanical tissue. The epidermis is heavily cutinized and the stomata are well protected within the epidermal layer both by their position and by the over-hang of their subsidiary cells.

FRANSERIA BIPINNATIFIDA NUTT.

HABITAT

This perennial is a sand binder and stabilizer rather than a dune former, although at times sand collects around the plants, forming small hummocks, the species being capable of withstanding slow burial. The highest rates of evaporation were obtained at the station where this species grew, indicating it existed under the most severe environmental conditions in the dunes as far as evaporation was concerned.

AERIAL PARTS

Franseria is a perennial whose ascending axis soon comes to be more or less reclining, the stems attaining a length of 2 to 3 feet. Branching is alternate or opposite, the internodes on reclining branches being three to four times as long as those on vertical branches. The alternate or opposite leaves, are twice to thrice pinnately dissected into irregular oblong lobes, and are canescent or almost silky with slightly recurved edges. The length of the leaf (blade and petiole) averages 5.0 cm., the length of the blade being about 3.7 cm. and its width 3.5 cm., while the thickness of the midrib, including the trichomes, is 0.90 mm., and without them, 0.60 mm.

SUBTERRANEAN PARTS

The root system is not extensive, reaching in most plants excavated to a depth of about three feet. Secondary roots are produced from the lower portion of the fleshy tap root.

ANATOMY OF THE STEM

The epidermal layer of the young stem, somewhat irregular in transverse outline, is covered with cuticle 0.002 mm. thick. Multicellular, unbranched, overlapping, pointed trichomes are frequent, often as long as twelve times the width of the epidermal layer. On the inner side of the epidermis of the younger stem the isodiametric cells of the cortical parenchyma contain chloroplasts; older stems have five to six rows of collenchyma inside the epidermal layer. In younger stems the cells of the cortical parenchyma become larger toward the center and, at intervals in this tissue, forming an irregular ring immediately outside of the vascular bundles and generally alternating with them, occur patches of specialized parenchyma cells with anthocyanin, giving the appearance of a duct, while in older stems no such disposition of anthocyanin occurs. In addition to these anthocyanin patches, there are located in the chlorenchyma groups of about two to four parenchyma cells containing anthocyanin in their cell sap.

The conducting system is a dictyostele with a group of sclerenchyma fibers on the outside of the phloem part of the bundle. The pith of the young stem,

distinctly of the herbaceous type, occupies over three-fifths of the diameter in transverse section, with druses commonly present in its cells. Later the cell walls of the pith thicken and become lignified, but the amount of pith does not decrease greatly with age (Pl. 10).

Anatomy of the Leaf

The adaxial surface of this diplophyll leaf is covered with a layer of cuticle 0.005 mm. thick, and the abaxial with a layer 0.003 mm. thick. The epidermal cells, 0.02 mm. in thickness, are heavy walled and of about equal size on both surfaces, each of which bears narrow, pointed, multicellular, unbranched trichomes. The tip cells of the trichomes are abruptly pointed or long pointed. Stomata, slightly sunken, are about 153 per square millimeter on the adaxial surface, and 150 on the abaxial, with a length of about 0.025 mm. and a width of 0.020 mm. Several rows of palisade cells occur under both the adaxial and abaxial surfaces, while in the center of the leaf are larger cells of spongy parenchyma containing here and there a few chloroplasts. These tissues, especially the large cells in the center of the leaf, contain an abundance of water, making the leaf succulent. Small druses are found throughout the mesophyll. In the region of the midrib the mesophyll consists of more or less rounded parenchyma cells, while in the rest of the leaf the mesophyll is of a more compact parenchyma containing a rather large proportion of elongated cells. In the vicinity of the midrib, on the adaxial surface, palisade chlorenchyma is lacking for a short distance, the space being occupied by parenchyma tissue, while on the abaxial surface there are two layers of palisade cells. Leaves vary in thickness in different locations in the dunes. Those near the strand were usually found to be two to three times thicker than those farther inland. The spongy parenchyma frequently becomes water accumulative in the thicker leaves.

Anatomy of the Root

On roots of approximately two mm. diameter the cork layer is three to four cells thick. The cortical parenchyma, composed of numerous thin-walled cells, contains a circle of schizogenous ducts. A few other similar ducts are scattered irregularly within this circle and occasional ducts are located outside of it. No differentiated endodermal layer was found. The conducting system is a dictyostele with the phloem and cambium well marked; the xylem contains some large tracheae and rather broad vascular rays; there is no pith.

Summary

Franseria, of the eleven species considered, grows under the severest dune conditions, under the highest evaporation rates, where there is little soil stability, with great exposure to wind and high temperature as well as to intense light. Under these xeric conditions the species shows the following modifi-

cations: low growth form; leaves much dissected and slightly recurved at the margin, presenting less superficial area; both sides of the leaves silvery, due to the presence of numerous overlapping trichomes which almost completely cover the epidermal surface. The stem is likewise covered with trichomes. The stomata, few per unit of surface, are slightly embedded in the epidermis. The root and stem contain some water accumulative tissue.

OENOTHERA CHEIRANTHIFOLIA HORNEM. VAR. SUFFRUTICOSA WATS.

HABITAT

This sand dune evening primrose is found on the upper portions of the strand beyond the storm-swept areas, and in stabilized locations farther from the ocean; it frequently grows alone in open sand areas, and also associated with *Abronia umbellata, Erysimum capitatum* (Dougl.) Greene, *Lupinus chamissonis* and *Eriogonum parvifolium*. Since it appears in bare areas and aids in stabilization, it may be classified as a pioneer, though it is of secondary importance in this respect, being less valuable than *Abronia maritima* and *Franseria bipinnatifida* in forming small dunes and in holding the sand.

AERIAL PARTS

Oenothera has a spread of about 2 feet, its branches radiating from a central rosette which crowns the taproot. The stems are mostly decumbent to prostrate, but when growing close to shrubs a plant may attain a height of one foot. It is somewhat woody near the crown.

The alternate leaves are thick and covered on both surfaces with short, dense, appressed trichomes, resulting in a silvery-canescent appearance. The shape of the obtuse leaf varies from obovate to oblong-lanceolate, with an entire or sinuate-toothed margin. On the basis of leaves collected at different seasons, the length of the leaf (blade and petiole) averages 2.0 cm., length of blade 1.8 cm. and the width 0.9 cm. The leaves which appear in spring are about twice as long as and considerably more flat than those produced during late summer and autumn. Upper leaves are sessile while the lower are usually petioled.

SUBTERRANEAN PARTS

The root system is a meager one. It consists of a tap root, slightly fleshy near the surface of the ground, extending to a depth of about three feet in an average specimen; it bears a few lateral roots (Pl. 11).

ANATOMY OF THE STEM

The epidermis, which contains anthocyanin, bears unicellular, unbranched trichomes of two sizes. The larger are in length about thirty times, while the

smaller are about ten times the diameter of the epidermal cells. The epidermis is covered with a layer of cuticle 0.002 mm. in thickness.

Below the epidermis are a few rows of isodiametric collenchyma cells. To the inner side of these is a region of slightly larger cells of cortical parenchyma, some of which contain bundles of raphides. A few rows of small chlorenchymatous cells enclose the stele. In stems of 2.0 mm. diameter, the stele shows a continuous cylinder of xylem, consisting mainly of tracheids with some small tracheae, without indication of separate vascular bundles. The vascular rays are very narrow and probably always uniseriate. The cells of the pith parenchyma are somewhat larger than those of the cortical parenchyma, and later become lignified; bundles of raphides occur in some. Many of the stems were found to be hollow.

Anatomy of the Leaf

Large, appressed, unicellular, unbranched trichomes cover both epidermal surfaces. They point toward the leaf tip, covering the blade. The small, rather thin-walled epidermal cells are similar on both surfaces, averaging 0.018 mm. in thickness. Cuticle, about 0.003 mm. thick on the abaxial surface is but slightly thicker on the adaxial. Stomata, lying even with the surface, are found on both epidermal layers. The guard cells average 0.025 mm. in length and 0.017 mm. in width.

The leaf is of the diphotophyll type with its mesophyll chlorenchymatous throughout. Below the adaxial epidermis are two layers of closely placed palisade cells. Below the palisade layers about one-half of the mesophyll is occupied by spongy chlorenchyma consisting of small, rounded, loosely disposed cells. The veinlets, surrounded by parenchymatous bundle sheaths, are numerous. Small bundles of raphides occur in the cells of the mesophyll while very large bundles appear to have extended themselves through several cells and intercellular spaces.

The leaf in cross-section averages 0.64 mm., including the trichomes, and without them 0.36 mm., while at the midrib the leaf measures 0.70 mm. with the trichomes, and without them 0.42 mm.

In plants of the more xeric conditions stomata average 170 to the square millimeter on the adaxial surface and 285 on the abaxial. On ten plants with larger leaves in a more mesic habitat, the stomata averaged 250 to the square millimeter on the adaxial and 354 on the abaxial surface.

In some instances, as in more mesic dune conditions, the diphotophyll type of leaf with two layers of palisade on the abaxial surface is displaced by the diplophyll with one layer of palisade under the abaxial surface.

Anatomy of the Root

The root develops several external layers of suberized cells. Its cortical parenchyma is probably for water accumulation, since the root becomes

slightly fleshy below the root crown. The well developed stele contains a small proportion of phloem, back of which lies the broad xylem zone containing numerous tracheae (Pl. 12).

SUMMARY

This evening primrose grows in the more xeric habitats of the sand dunes. Its structural modifications are shown chiefly in its growth-form and somewhat in its internal anatomy. It is low growing and well-rooted. The leaves, slightly fleshy, are silvery-gray in color, being covered with a thick layer of overlapping trichomes. Many of the leaves are shed during the dry season. The palisade layers are compact and aid in reducing transpiration.

LUPINUS CHAMISSONIS ESCH.

HABITAT

Lupinus is not found on the strand or in the foredunes, and while it grows on the most exposed areas in wind swept blow-outs and often on the very crest of the dunes, withstanding there the severest winds, it becomes established best in locations where the wind is not active in moving the sand and in areas where establishment of other species has already taken place. From atmometer readings at stations near Lupinus, evaporation rates were found to be less than in communities of *Abronia maritima* on the strand. The Rhus community, however, has a lower and less variable evaporation rate. Lupinus is found alone in wind swept areas or associated with Ericameria, *Abronia umbellata* and Eriogonum in partly stabilized sections.

AERIAL PARTS

This erect woody evergreen shrub, with numerous stout branches which are leafy throughout, attains a height of 4 to 5 feet and a horizontal extent of about four feet. The alternate leaves are palmately compound, consisting of four to nine leaflets which are somewhat folded, forming a V. The leaflets are cuneate-obovate, obtuse to acute, and silky on both sides. The petioles are dilated at the base and bear at the upper end of the dilation two stipule-like lanceolate appendages at either side of the petiole. The length of the leaf averages 2.5 cm., the leaflet blade on the average being 1.6 cm. in length with a width of 4.2 mm. The autumn aspect of the species shows the leaves more V-shaped in cross-section and more rolled than in other seasons.

SUBTERRANEAN PARTS

The root system is very extensive; one plant 2 feet in height had a root spread of 13 feet at a depth of 11 feet, this representing an average condition. The customary tubercles of leguminous plants occur on the roots (Pl. 13).

ANATOMY OF THE STEM

The epidermis of the young stem, covered with cuticle 0.004 mm. thick, bears closely placed, exceedingly long, unbranched, multicellular trichomes. On stems, whose diameters are slightly over 1.0 mm., the trichomes are as long as the stem is wide, being exceeded in length in the other species studied only by occasional trichomes on the stem of Oenothera. The trichomes consist of an enlarged epidermal cell, a short stalk cell, and a long filiform terminal cell. To the inner side of the epidermis occurs one, or sometimes two, rows of chlorenchyma and below this tissue are several rows of large cells of cortical parenchyma. From the sclerenchyma areas at the outer ends of the vascular bundles, as seen in cross-section, there runs a more or less continuous ring of sclerenchyma. Pith, consisting of large cells, composes about one-half of the cross-section of the young stem, while the older stem becomes woody, with a large cylinder of xylem in which there is an irregular development of tracheae in a cylinder composed principally of tracheids (Pl. 14).

ANATOMY OF THE LEAF

The epidermal layer of a leaflet is about 0.015 mm. thick on each surface, covered by cuticle about 0.003 mm. in thickness varying to about 0.002 mm. on the abaxial side. Both surfaces of the blade, and the petiole with its extensions, bear a large number of long, narrow, unbranched, multicellular trichomes, in total length about seven times the width of the epidermis. They consist of an enlarged epidermal cell, a short stalk cell, and a long terminal cell.

The stomata projecting slightly beyond the epidermal surface, average about 150 to a square millimeter on each side of the leaf and measure about 0.030 mm. in length and 0.025 mm. in width. The entire leaf inside of the epidermis is composed of rather closely placed palisade tissue, except at the center, where there is some spongy chlorenchyma in which are veins surrounded by a parenchymatous sheath. The conducting system is composed of one large vascular bundle at the midrib, which is one-fourth the thickness of the leaflet at that point, and of a number of smaller bundles distributed through the center of the leaf. The leaf measures about 0.35 mm. in thickness exclusive of the trichomes, and with the trichomes 1.10 mm.

ANATOMY OF THE ROOT

The younger root is covered with a small amount of cork and contains a wide layer of cortical parenchyma; in the older root the latter becomes much reduced with the increasing width of the xylem. The phloem is rather small in size while the xylem contains a liberal number of rather large tracheae, and has conspicuous one to three-seriate vascular rays extending well out into the cortex.

SUMMARY

Lupinus is found in stabilized areas or sometimes occupies the same position in the dunes as does Franseria in the more exposed positions where the greatest evaporation and the severest conditions of instability prevail. The root system is very widespread and deep, the most extensive of those investigated. Instead of broad leaves it has V-shaped leaflets, as seen in cross section, offering less surface exposure to the sun, and becoming thereby much less rapidly heated. The leaves, like those of Franseria, are covered with overlapping trichomes, resulting in a silvery appearance and providing a still air space between the trichomes and the epidermis. Due to the abundance throughout of palisade tissue, the leaf is compact with very little intercellular space, and loss of water is consequently reduced. The young stems bear long filiform trichomes, giving them a silvery appearance similar to that of the leaves.

ERIOGONUM PARVIFOLIUM SM.

HABITAT

This woody perennial shrub, sometimes attaining four feet in height, occurs not only on the sand dunes, but also on the hillsides near the coast. In the dunes it is found on stabilized sand or on hummocks in unstabilized areas, usually where Franseria has already become established. Its other common associates are the species of Rhus, Lupinus, Ericameria and *Abronia umbellata*, though with respect to these other dune plants, Eriogonum may be considered as of secondary importance.

AERIAL PARTS

The shoot system has a spread of about 3 feet, and is made up of stems that are white-tomentose when young, becoming reddish with age, the alternate branches bearing densely fascicled leaves.

The leaves are oblong-lanceolate to ovate, obtuse, truncate to subcordate at the base, the margin undulate and irregularly revolute. The peculiarities of this margin, a conspicuous feature of the leaf, are most noticeable in autumn. Young leaves are covered with a mat of intertwined hairs on both surfaces; at maturity they are very dark green and shiny above, and covered with a dense white felt beneath. The length of the leaf (blade and petiole) is about 2.7 cm.; the blade, 1.2 cm.; its width about 1.2 cm.

The young petiole is short and broad, clothed with trichomes on the abaxial surface and less abundantly so on the adaxial; in maturity the petiole becomes less flat, longer and less hairy.

AERIAL PARTS

This sand-verbena is prostrate, with very slender stems about 3 to 5 feet in length, widely branching from the crown of a fleshy root. On several occasions it was observed that Abronia, growing in rather dense vegetation, had changed from its prostrate form to a climbing form in scrambling over a shrub. Its vegetative growth, with its slender stems and slight leaf development, is inadequate to cope with sand movement as compared with the sturdy growth of *Abronia maritima*. The height of the aerial portions, which is generally about 4 to 5 cm., depends on the total length of the leaf when the stems are prostrate, as is usually the case.

The stem is viscid-puberulent, generally reddish, with long internodes and opposite branching.

The leaves of a pair are unequal. They are flat, thick, obtuse, broadly obovate to oblong, with slightly sinuate margins. The position of the leaves is more or less vertical from the prostrate stem. The mature leaf (including blade and petiole) is about 4.0 cm. in length. The length of the blade is 2.3 cm., the width 2.3 cm., and the thickness 1.1 mm.

SUBTERRANEAN PARTS

The root system is more extensive than in *Abronia maritima,* and there is not so much burial of stems by sand in *A. umbellata*. When, however, the wind causes an accumulation about established plants they become partially covered. The spreading of the plant from its center is brought about by means of aerial and not underground portions. The tap-root, fleshy just below the surface of the soil, may extend to a depth of 4 to 5 feet. Lateral roots spread one to three feet from the tap-root (Pl. 17).

ANATOMY OF THE STEM

The stem is composed largely of water accumulative tissue. Its epidermis, bearing infrequent stomata, is 0.01 mm. thick, covered with cuticle 0.002 mm. thick, and with a scattering of multicellular glandular trichomes. Anthocyanin may be found in the epidermal layer.

The cells of the cortical parenchyma, some of which contain chloroplasts, are about two times the diameter of the epidermal cells. Bundles of raphides of calcium oxalate are present in some. On the upper side of the stem the cells contain more chloroplasts than do those on the lower side, due to greater exposure to light.

The endodermis is clearly differentiated. Solereder (1908) states that a ring of cambium inside of the pericycle produces on its inner side secondary collateral vascular bundles and parenchyma tissue. The parenchymatous cells are pitted, giving them the appearance of woody tissue. Pith, with some cells containing bundles of raphides, occupies the center of the stem in which

is disposed a ring of separate vascular bundles. Little mechanical tissue is present.

ANATOMY OF THE LEAF

The diplophyll leaf is made up chiefly of palisade tissue. Its epidermis is covered with a layer of cuticle, 0.003 mm. thick, and bears a few multicellular glandular trichomes, which have spherical heads larger than the cells of the stalk. The epidermis, with anthocyanin in most of its cells, is 0.025 mm. thick, being practically the same on both sides of the leaf. The epidermal cells are round to rectangular, except that those serving as bases for the hairs are larger and somewhat triangular in the leaf cross section.

The remainder of the leaf is composed of chlorenchyma, in which there are about six rows of palisade. Regularity of palisade tissue is not as prominent a feature in Abronia as in the leaves of the other species investigated. Numerous chloroplasts, some bundles of raphides, and considerable water are found throughout the palisade. Within the leaf blade are a few cuboid cells of spongy chlorenchyma, and small vascular bundles, around each of which is a parenchymatous bundle sheath (Pl. 18).

About 50 slightly sunken stomata per square millimeter occur on the adaxial surface and about 60 per square millimeter on the abaxial. Their guard cells are 0.040 mm. long and 0.025 mm. wide. The epidermal cells of the petiole of the leaf and the edges of its blade contain conspicuously more anthocyanin than do the epidermal cells of the general leaf surfaces.

ANATOMY OF THE ROOT

The fleshy tap-root bears a corky layer which is comparatively heavy without being bark-like in character, at least within the limit of present observations. The cortical parenchyma is composed of large thin-walled cells about six cells thick in roots 2.0 mm. in diameter. The remainder of the root structure is the same as in *A. maritima*, with pith parenchyma and a concentric arrangement of secondary vascular bundles. Bundles of raphides are present. There is but little phloem and the xylem contains few tracheae.

SUMMARY

The species conserves water by a low habit of growth, vertically placed leaves, small number of stomata per unit area, presence of cuticle, compact tissue of palisade character, and a small amount of intercellular space. The plant is adjusted to the sand dune environment somewhat differently than its close relative, *A. maritima*, in possessing less succulence and a deeper root system. *A. umbellata* conserves water by the death of the older leaves during the dry part of the year, while in *A. maritima* only a few leaves die then. *A. umbellata* produces seeds abundantly, propagating by this means rather than vegetatively, as does *A. maritima*. *Abronia umbellata* is not as succulent, has fewer trichomes and more stomata per unit area than *A. maritima*.

ERICAMERIA ERICOIDES (LESS.) JEPSON

HABITAT

Ericameria is found for the most part in locations where there are sand dunes somewhat removed from direct wind action, and the species is one that can endure some covering by sand. It is associated with those plants which come into the partly stabilized dune areas, such as Lupinus, Eriogonum and Rhus. Occasionally, *Lotus scoparius* (Nutt.) Ottley, *Abronia umbellata* Lam., *Galium angustifolium* Nutt., and *Erysimum capitatum* (Dougl.) Greene are associated with it.

AERIAL PARTS

This evergreen shrub attains an average height of about 3 feet. Its main stems are mostly upright while the peripheral branches often become decumbent and yet have numerous erect branches, making the plant about 4 feet wide. Ericameria has a xeric appearance, with a heather-like herbage of alternate linear-terete leaves. The somewhat pubescent leaves and stems are resinous. The leaves, occurring in fascicles, are somewhat vertically placed, the lower leaf being longer than the others, averaging a little less than one centimeter. Measurements of the lower leaf made after the rainy season averaged 1.4 cm. in length, while the other leaves, placed between this and the stem, averaged less than 1.0 cm. The thickness from the dorsal to the ventral surface of a leaf averaged 0.56 mm. and its width 0.70 mm.

SUBTERRANEAN PARTS

The root system is extensive, the tap and secondary roots extending downward eight or more feet into the soil in an average adult specimen, while the horizontal spread of the roots is about five times as great as the spread of the aerial parts. The roots grow uniformly in all directions at the different depths of their distribution (Pl. 19).

ANATOMY OF THE STEM

The stem is very tough and woody, even when young, and while young its epidermis bears long filiform trichomes of about three cells, consisting of one or two small cells near the surface and an extremely long terminal cell. Cuticle, about 0.002 mm. thick, covers the surface. There are about 40 stomata per square millimeter. Beneath the guard cells and the adjacent protruding epidermal cells, large stomatal chambers occur. In the older stem there is a superficial development of cork, and in the younger stem, below the epidermis, a narrow band of cortical parenchyma in which are bundles of acicular crystals and resin canals apparently of schizogenetic origin. A group of sclerenchyma cells is located outside of the phloem part of each vascular bundle. The stem is of the dictyostele type with collateral bundles, the xylem,

with a few tracheids and numerous small tracheae, is well developed. The frequent vascular rays are conspicuous, being three to four cells in width. The central pith, with a few cells containing bundles of acicular crystals, is small and definite, occupying about one-fifth of the diameter of the stem, as seen in transverse section in the specimens examined (Pl. 20).

Anatomy of the Leaf

The minute needle-like leaves, are terete, with a groove on the adaxial side. The epidermis, having numerous filiform trichomes when young and entirely smooth when old, is 0.030 mm. thick, and is covered with a layer of cuticle 0.005 mm. thick. The guard cells are about even with the epidermis. Stomata, arranged in rows, are present on all sides of the leaf, and possess large stomatal chambers. The stomata average approximately sixty per square millimeter, and are about 0.010 mm. long and 0.006 mm. wide. Nearly three-fourths of the leaf tissue is composed of dense palisade in which are acicular crystals[16] of calcium oxalate.

The center of the leaf is occupied by spongy chlorenchyma which also partly surrounds the three resin canals; close to these, the three vascular bundles composing the vascular system are located.

Leaf size varied in different locations in the dunes, being larger than the average on plants located near the ocean, and owing this increased size mainly to a larger proportion of palisade tissue.

Anatomy of the Root

Young roots develop a cork layer inside of which are a few rows of small cells of cortical parenchyma, whereas older roots are covered with bark. The root is of a woody type, the xylem, with conspicuous vascular rays and a row of resin-canals, occupying more than one-half of the diameter. There is no pith.

Summary

Ericameria, although found in less xeric habitats than *Abronia maritima* and Franseria, does not occupy the most mesic position in the sand dunes. It has been pointed out elsewhere that when evaporation rates increased at all the stations, these rates were greater at the Ericameria station than at the Rhus station. When the evaporation rates decreased at all other stations, they were also less in the Ericameria, but were usually lower there than at the Rhus station. In other words, there is greater fluctuation at the Ericameria than at the Rhus station. Ericameria is usually found in the stabilized dune areas where there is little movement of the sand, and where the vegetation grows in rather open stands, spaced so as to insure an adequate water supply. The shape of its microphyll leaf gives small surface exposure

[16] According to Solereder (1908), "True raphides are wanting, but occasionally the bundles of acicular crystals come to resemble bundles of raphides."

in proportion to the leaf volume. A heavy cuticle covers the fascicled leaves, while long trichomes cover the younger stems.

RHUS INTEGRIFOLIA B. & W.

HABITAT

This evergreen shrub grows not only in sand dunes but also on clay bluffs along the coast and for some distance inland. In the dunes it is located on stabilized areas, growing best where there is little direct wind. The species is propagated mainly by vegetative means, forming extensive thickets frequently 30 to 40 feet in diameter, with some approximately 100 feet. On older plants the lower branches become procumbent and often take root where they come in contact with the soil.

AERIAL PARTS

The shrub grows to an average height of 5 feet, and in sheltered places may become taller. Plants on the summit of a dune frequently are scarcely 6 inches high while on the leeward side they may attain a height of 6 or more feet. Where the wind commonly has a rather high velocity, the shrub acquires a flat top, with the tips of the twigs dead; this is probably due to the drying effect of wind on the terminal buds. Communities of the plants spread out on the lee slopes of dunes at right angles to the general direction of the wind, seldom becoming circular in outline.

The alternate twigs are stout and stiff. Often in exposed locations dead twigs are found on the windward side of a shrub. At the Silver Strand two lichens, a variety of *Ramalina ceruchis* (Ach.) De Not. and *Dendrographia minor* (Tuck.) Darb., grow on such dead branches.

The leaves are mostly vertically placed, leathery, alternate, elliptic and obtuse. The margin is entire or with a few sharp teeth, which appear to develop on plants of the more xeric locations, though this characteristic is not constant. The leaves (blades and petioles) average 4.5 cm. in length, the blade 4.3 cm. in length, its width 3.1 cm. They are very shiny, doubtless thereby reflecting much light. The color of the adaxial surface is dark-green, while that of the abaxial is much paler. The veins are conspicuous (Pl. 21).

Vegetative reproduction appears to be more frequent and effective than reproduction by seeds. Birds have been noted carrying seeds, but no seedlings and few young plants were observed.

SUBTERRANEAN PARTS

The root system, consisting of a tap-root and an abundance of long secondaries, is extensive, especially when the plant occurs in large thickets. Some of the secondaries extend 10 feet beyond the periphery of the aerial

portion of the shrub. Many of the heavy laterals become exposed through the action of high winds. Adventitious roots occur on procumbent, partly buried branches. Shapiro and de Forest (1932) found that the species is a highly conservative user of soil water.

Anatomy of the Stem

The younger stems are covered with cuticle 0.003 mm. in thickness and bear numerous, unicellular, rather thick-walled, unbranched trichomes which, when fully grown, are in length from five to ten times the diameter of the epidermal cells; the stomata are slightly depressed. At the inner side of the epidermis are several rows of rather thin-walled collenchyma, anthocyanin being present in about six rows but principally in the one adjacent to the epidermis. The remainder of the cortex is occupied by rather small, thin-walled parenchyma cells in which are occasional druses of calcium oxalate (Pl. 22).

A single, large resin canal, partly surrounded by a zone of sclerenchyma, is located in the outermost part of each vascular bundle, in which neither phloem nor xylem is well developed. Tannin was found in the stem. The biseriate or triseriate rays are narrow, and the pith is composed of comparatively small parenchyma cells, some of which contain druses. The most striking features of the stem are the smallness of its cells, the small amount of conducting tissue, and the absence of water accumulative tissue.

Anatomy of the Leaf

The leaf is covered on both surfaces with a thick layer of cuticle, especially on the adaxial side, where it is 0.007 mm. thick, while on the abaxial it measures but 0.004 mm. The adaxial epidermis is 0.037 mm. in width, the abaxial 0.030 mm. The cells are oblong and wider at the surface adjacent to the mesophyll. The stomata, which occur only on the abaxial surface, average 255 to the square millimeter, with guard cells 0.030 mm. long and 0.025 mm. wide. The epidermal cells abutting upon the guard cells are somewhat modified. The epidermis of the abaxial surface bears infrequent, unicellular, unbranched, slightly pointed trichomes, in length about five times the width of the epidermis.

This diplophyll leaf has two layers of well developed, closely placed palisade, below which may be a poorly developed third layer. The first two layers occupy less than one-half of the mesophyll. The rest of the mesophyll consists of irregularly shaped cells, some being somewhat palisade-like in character. Druses of calcium oxalate are present in the mesophyll.

With the vascular bundle of the midrib is associated a large resin-canal, surrounded on the lower portion by several rows of sclerenchyma which extend around the xylem and are continued beyond it to the adaxial epidermis

as a strengthening bar. Veinlets also have resin-canals and sclerenchyma associated with them. Anthocyanin is present in several rows of collenchyma of the petiole, in cells inside of the abaxial epidermis at the midrib, and in groups of cells in the margin of the blade. The margins of the leaf are strengthened by sclerenchyma.

Anatomy of the Root

From a phellogen originating in the outer third of the cortex a good development of suberized tissue arises. Within the cortical parenchyma a number of large schizogenous resin passages occur. The phloem is poorly developed. In the xylem, scattered among the tracheids, are well developed and numerous large tracheae; the small vascular rays are mostly uniseriate.

Summary

Rhus integrifolia, the least xeric species of those considered, is more distinctively a member of the chaparral component of the broad-sclerophyll communities of southern California than of the sand dune vegetation. The leaves mostly maintain acute angles with the stem, thus somewhat reducing exposure to light. Both surfaces are well protected by cuticle, which, in addition to the thick outer epidermal wall, renders the leaf stiff. The leaf tissues are compact, especially the palisade below the adaxial surface. The stem and the root are compact in structure, owing chiefly to the smallness of most of the cells. It is probable that the sclerenchyma arranged in a half-column around the vascular bundles aids in maintaining rigidity when there is a deficiency in the water supply. A branch cut and left lying on the sand in the month of June seemed, after a week of exposure, to be as fresh as branches on the shrub.

Rhus integrifolia appears to represent something of a transition between the customary species of a dune complex and those of the chaparral. The stations where Rhus occurs show the greatest stability of the sand and the lowest rates of evaporation as compared with all other stations.

SUMMARY OF AUTECOLOGICAL DATA

Introduction

The sand dune species of southern California may be divided into two groups: (1) annuals, biennials, or root perennials whose aerial parts appear after the winter rains—growing, blossoming and fruiting, then withering when the dry season approaches; and (2) woody, suffrutescent and succulent perennials which maintain aerial parts throughout the year, even in the most unfavorable period.

Extended consideration will not be given to the first group, since, because of their growth habits, they escape the severe conditions of the habitat during

the unfavorable portion of the year and, consequently, do not exhibit structures suited to such a period, as do the plants of the second group.

GROWTH HABITS

The growth forms in the southern California dunes differ in certain respects from those in some other dune areas. Cowles (1899) has shown that trees, such as the basswood-maple series in the Michigan dunes, form a part of the development. In the Philippines, Kienholz (1926) refers to trees on the upper beach in his study of the beach vegetation, and Cooper (1922) has shown the part trees play in the succession in coastal dunes at Monterey. No trees are present, however, on the southern California coastal dunes. The shrubs for the most part are low and in wind-swept places present a "krummholz" appearance. Portions of some plants exposed to the windward west side of slopes are often much stunted or dead. Where the sand action is pronounced, woody stems sometimes exhibit sand blasting of the bark, and, indeed, some similar effect appears to show occasionally on the leaves themselves. Suffrutescence, though not so markedly developed in the sand dunes as elsewhere, is a characteristic of most of the southern California cismontane vegetation. Oenothera, for example, shows definite suffrutescence. Of the eleven sand dune species investigated the shrubs are low, often decumbent, sometimes spreading and forming thickets over large areas, as in the case of Rhus. The succulent perennials are evergreen and mostly prostrate.

Certain stages in dune development support certain growth forms. There are no shrubs near the strand or in the fore-dunes. These small dunes are held entirely by evergreen perennials, principally *Abronia maritima*, and, to some extent, by the Franseria and the Atriplex. These species are the principal pioneers, especially *Abronia maritima* and Franseria, and are exposed to the most xeric conditions. Couch (1914) in making quadrat studies at Manhattan Beach, Los Angeles County, California, in 1913, found Franseria as a pioneer, followed by *Abronia umbellata* in protected areas. Over flat areas between the hummocks of sand Convolvulus spreads by means of its rhizome habit, acting as a pioneer and stabilizer.

In the moving dune areas Franseria and Lupinus are present. Few annuals are found there, probably owing to the unstable substratum. Active wind movement, soil instability, intense heat and light, and high evaporation rates contribute to the xeric conditions. After pioneers, such as Abronia or Franseria, are more or less established, other species appear as invaders. *Abronia umbellata*, Oenothera, and Eriogonum are chief among these. Such invasion occurs on hummocks in the moving dunes.

Mesembryanthemum plays diverse rôles. Sometimes it is a pioneer just back of the strand, sometimes it is an invader of practically stabilized areas, and sometimes it covers large areas on the leeward slopes of the more or less stabilized dunes.

Still farther removed from the ocean, where wind action is decreased, reflected and diffused light lessened, and the soil relatively stable, shrubs occur in open stands, growing to a height of 4 or 5 feet. Couch (1914) at Manhattan Beach, Los Angeles County, in 1913, found *Abronia umbellata* dominant in one quadrat, with Eriogonum and Lupinus apparently almost codominant in another, while in a third, *Adenostoma fasciculatum* H. & A., was dominant. He states that this last appeared "suddenly," being peculiar to the summit and leeward slopes, but absent from the windward slopes. In the present investigation no succession was encountered in any of the dune areas of southern California in which Adenostoma represented the climax, nor was the species found in any stage leading thereto, although reported by Whitfield (1932) as occurring in Santa Barbara County. Specimens were collected, however, north of southern California in the sand dunes at Seaside, Monterey County, and in areas farther north.

The principal shrub species of the general sand dune complex in southern California are Lupinus and Ericameria, with large, spreading thickets of Rhus in the most mesic habitats.

Along the southern California coast, at several points, true halophytes, such as species of Salicornia, are floristic components of the vegetation of small areas. This does not indicate that the dunes are halic, as explained by Kearney (1904). In the sand these plants showed poor development and were not successful in withstanding covering. They appeared to be relics of an earlier habitat condition. In a saline area on the bay side of the Silver Strand they had become established; then followed an unusual amount of sand movement in which they became partially covered. These plants are now yellow in color and in a dying condition.

Shoot Systems (Leaf and Branch)

Stems are of two characters, one with enough stiffening material to stand erect, as in the shrubs Rhus and Ericameria, and the other with little mechanical tissue, as in the case of the Abronias and Convolvulus. Stems of Convolvulus, *Abronia maritima*, *A. umbellata*, and young stems of Mesembryanthemum are very succulent. Variation in surface texture occurs from smooth and shiny in young stems of Mesembryanthemum; silvery-canescent, as in young stems of Lupinus, to cork and bark development in the shrubs, such as Rhus and Ericameria. Growth in length is not rapid in the shrubs, short internodes being characteristic.

Leaves for the most part are small as in Eriogonum and Ericameria; Franseria has lobed leaves; the leaves of Mesembryanthemum are equilateral, while Lupinus has its leaflet blade partly folded. Some leaves have revolute edges, as Eriogonum. Mesembryanthemum, with its thick equilateral leaves, shows the highest degree of succulence; *Abronia maritima* is invariably suc-

culent, though the character of its flat leaves renders this feature much less pronounced than in the former species. *Abronia umbellata* and Franseria are not so succulent, but when growing in areas near the ocean, as at the Silver Strand, they develop this quality to some degree. Convolvulus varies considerably, depending upon the quantity of water accumulative tissue.

WATER CONTENT OF SPECIES

A comparison of the percentages of water in the shoot and the root systems of the representative species was made in August, 1932. Three plants of each species were excavated, the shoot system severed from the roots, each being weighed in the field immediately. Shoots and roots were placed in separate labeled containers and sun-dried for a week. Then they were placed in an oven at 100 to 105°C. until a constant weight was reached. The percentages of water were computed upon a dry weight basis, using:

$$\frac{\text{wet weight - dry weight}}{\text{dry weight}} \times 100 = \text{percentage of water in plant.}$$

Referring to Fig. 7, Convolvulus, Mesembryanthemum, the Abronias, Franseria, and Oenothera had the highest percentages of water in their shoot systems. Their root systems also ran with high percentages, with the exception of Mesembryanthemum. These species are rather shallow rooted, growing in the more exposed situations in the dune habitat. Ericameria and Eriogonum had the lowest percentages of water in their shoot systems and almost as low percentages in their root systems. These species are more deeply rooted, reaching to layers of sand which remain moist for longer periods after rains.

ABSORPTION OF WATER BY AERIAL PARTS

Absorption of water by the shoot system has been demonstrated by a number of investigators. Marloth (1908-10) and Schönland (1908-10) working in South Africa on the same plants, *Mesembryanthemum barbatum* L., *Crassula cymosa* L. and *Anacampseros filmentosa* Sims., arrived at opposite conclusions in regard to leaf absorption. Demaree (1931) demonstrated absorption in *Taxodium distichum* (L.) Richard, *Sequoia sempervirens* (Lam.) Endl., *Cynara cardunculus* Linn., and in species of Ailanthus, Vitis, Aesculus, Eucalyptus, Quercus and Salicornia. Dandeno (1901) states,

> Special parts of leaves of certain plants seem to be adapted to the purpose of absorption as shown by the surface of the epidermal cells over the veins, at the base of the trichomes, and in other regions. Trichomes in some cases are particularly susceptible to the action of water and of solutions applied to them. Striations and hairs or trichomes aid in spreading liquids over the regions which seem to be adapted to absorption; and trichomes prevent a rapid evaporation of the liquid so spread, by retaining air. Absorption of water may take place also through the surface of the petiole.

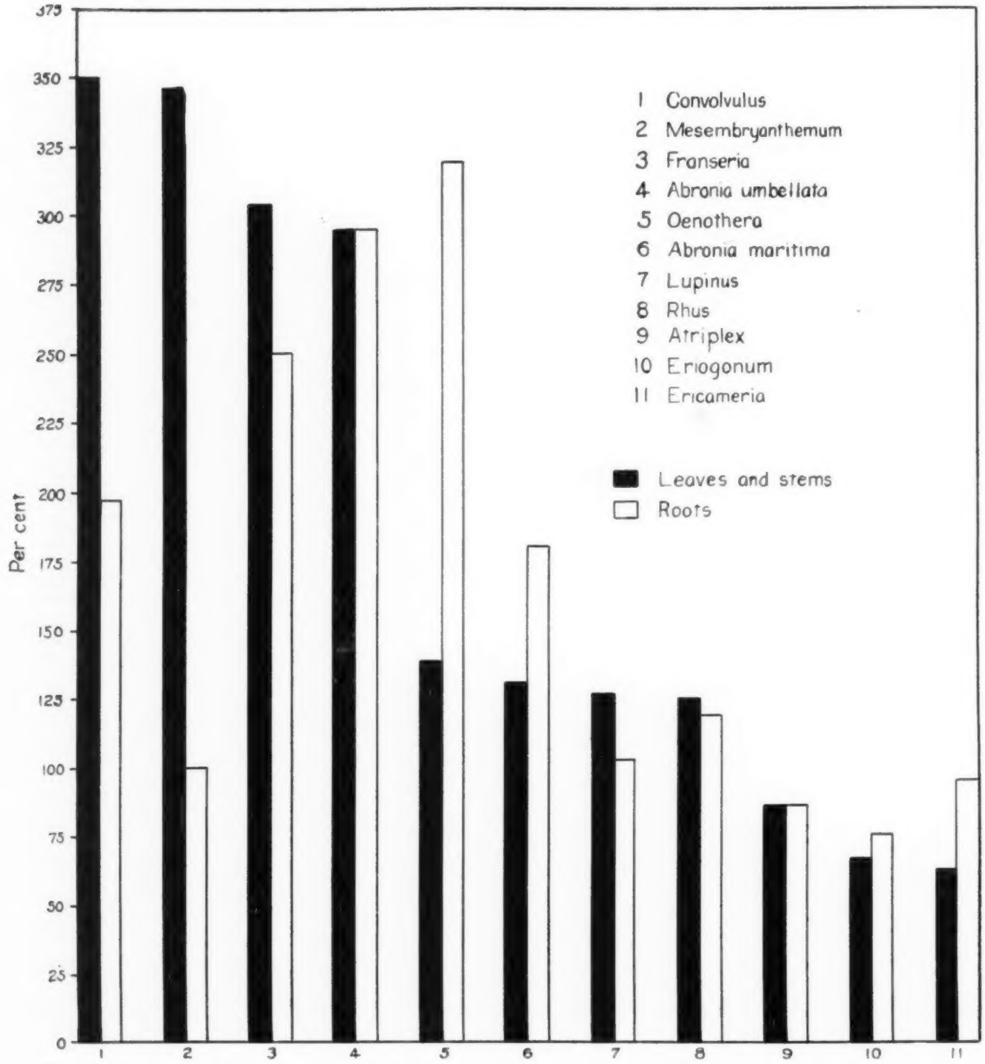

FIG. 7. Percentages of water in leaves and stems compared with roots of eleven dune species (calculated on the dry weight basis).

The method used by the writer, which may be called the direct method, was an attempt to ascertain whether a water deficit existed in any of the eleven species during August, 1932. If a deficiency existed in any plant, and water was available through the aerial portions, it might be absorbed through this channel since it was not available through the usual agent of absorption, the root system. The quantity absorbed per unit of surface was not determined.

At the time of the experiment the plants at both El Segundo and on the Silver Strand had received no moisture in the form of rain for over 3 months. The procedure was as follows: Into quart bottles of distilled water in which 100 mg. of eosin had been dissolved, there were immersed healthy branches

attached to the plants growing in their habitat, care being taken not to use mutilated or cut leaves or stems. A thin film of oil was placed over the surface of the water to prevent evaporation, and a file mark on the neck of the bottle indicated the water level. After several tests a period of 24 hours was decided upon as being the most suitable, at the expiration of which the amount of water withdrawn was determined. The specimens were then removed to the laboratory, dried and sectioned.

A water deficit was apparent in each of the eleven species in August, 1932, otherwise they would not have absorbed water through their aerial parts.

Root Systems

These may be conveniently grouped into systems with (1) well-developed main root, as in *Abronia umbellata*, (2) those with both main root and laterals well developed, as in Rhus, and (3) those with short roots superficially placed, as in Mesembryanthemum. Almost all the systems excavated showed, however, a considerable depth as compared with the height of the aerial parts of the plant. A few of the tap-roots were fleshy, as in Franseria, while Convolvulus had a well developed rhizome habit. No bulbous plants were found. The data gathered agree with Cannon's (1924) observation in South Africa. He says:

> The sclerophyllous species all appear to have roots which vary to a certain and possibly usually considerable degree as regards the depth and lateral extent of development, but they all agree on having relatively large development of the root-systems.

The succulent habit, as a rule, is accompanied by a meager root-system. After a heavy rain with practically no run-off, the sand surface soon dries by evaporation, the soil below maintaining its moisture for some time partly because the upper layer of dry sand reduces capillary action. Moisture by its retention in the plant body is available for use in succulents long after the rains cease. In the dunes, when the plant possesses little or no succulence, the depth of the root system increases.

Root length may be influenced, however, by other conditions than the amount of soil water. Cannon (1925) states that the branching of roots occurs whenever there is sufficient oxygen in the soil to permit root-growth. Waterman (1919) in his work on root systems of Lake Michigan sand dune plants from the viewpoint of their development, finds that their reactions are specific and hereditary. He believes that the evidence points conclusively to nutrient, or at least to chemical influences, as the cause of variability in symmetry of root extension under dune conditions. In the present investigation there is a noticeable variability in the form and the development of the root system of each species. Weaver (1919) finds that plains species under dune conditions develop roots of less depth than such species not growing in dunes.

Aside from these influences, others may be the chemical composition of the soil and the soil temperature.

Because the substratum in much of the dune area is of a shifting nature, plants growing there must be able to accommodate themselves to this instability if they are to grow there at all. One means by which this instability is withstood is the production of adventitious roots on stems when these are buried by sand. Many species are rooted deeply enough to attain a moist soil layer that remains moist all through the long dry season. *Abronia maritima* is the principal pioneer and dune former, while Franseria is a stabilizer of flat surfaces. Rhus has its lower branches procumbent, these sometimes taking root at the nodes. Adjustments, in other words, are made in different ways.

ANATOMY OF THE STEM

The stems may be placed conveniently in two groups, namely, those which have much water accumulative and little mechanical tissue, and those which are woody. The cortical parenchyma of the Abronias and Mesembryanthemum constitutes a wide band composed of water accumulative tissue. The woody stems, on the other hand, have a narrow cortex and an extensive development of xylem, as in Ericameria. Those with water accumulative tissue usually have a large proportion of pith; woody stems have a small amount, even when young.

There is considerable variation in the epidermal covering. Most of the young stems possess a layer of cuticle. While Mesembryanthemum and Convolvulus have a smooth epidermis, *Abronia maritima* and *A. umbellata* bear glandular trichomes. Young stems of Eriogonum, on the other hand, have both glandular and non-glandular trichomes, while only the non-glandular occur in Ericameria, Franseria, Lupinus, Oenothera and Rhus. Atriplex bears vesicular trichomes. The frequency of such outgrowths varies from a scattering to a dense covering, giving a silvery appearance to the stems of some species. Older stems of the woody forms develop a suberized layer. Anomalous structure occurs in the vascular tissue of *Abronia maritima*, *A. umbellata*, Atriplex, and Mesembryanthemum, where a ring of cambium has developed concentric circles of xylem separated by parenchyma. These are probably genetic variations.

The percentage of the stem devoted to tracheids and tracheae, and the relative proportion of each, vary with the age of the individual as well as with the species itself. The Abronias, Atriplex, and Convolvulus contain a small number of tracheae. In Mesembryanthemum they are exceedingly small in size as well. The phloem always constitutes a very small portion of the vascular bundle, being on the outside of it except in Convolvulus where the bundles are bicollateral.

Anthocyanin is present in, or just below, the epidermal layer in *Abronia*

umbellata, Atriplex, Franseria, Convolvulus, Mesembryanthemum, Oenothera, and Rhus.

Crystals of various types commonly occur in the cortical or pith parenchyma. The most usual form is that of bundles of raphides, as in *Abronia maritima*, *A. umbellata*, Mesembryanthemum, Oenothera; acicular crystals are found in Ericameria and druses in Atriplex, Franseria, Eriogonum and Rhus. In Convolvulus and Lupinus none were in evidence during the investigation.

Mechanical tissues, in the forms of sclerenchyma and collenchyma are, of course, present in many of the stems. Rhus has sclerenchyma in the form of arcs around each resin duct of the phloem portion of the vascular bundles. In plants with anomalous structure, *Abronia maritima*, *A. umbellata*, and Mesembryanthemum, the unusual disposition of xylem instead of distinctively mechanical tissue apparently provides sufficient support.

Stomata are not numerous in the stems of any of the herbaceous species; some are slightly sunken.

In the stems of all eleven species intercellular spaces are noticeably small in size and reduced in number.

Chloroplasts are diversely dispersed in the cortical parenchyma. In some species, as in *Abronia maritima* and Mesembryanthemum, they are distributed throughout this parenchyma, while in others, as in *Abronia umbellata*, they occur irregularly in the few rows of parenchyma immediately beneath the epidermis, or, again, as in Atriplex, they are in cells arranged in small groups in the cortex.

TABLE 9. Summary of structural features of the stem.[17]

Species	Succulent	Suffrutescent	Woody	Tracheae		Tracheids		Water accumulative tissue		Collenchyma	Sclerenchyma	Inclusions		
				Numerous	Few	Numerous	Few	Present	None			Crystals	Latex	Resin
Abronia maritima	x[18]	.	.	.	x	.	x	x	.	.	.	x	.	.
Abronia umbellata	x	.	.	.	x	.	x	x	.	.	.	x	.	.
Atriplex	.	x	.	.	x	.	x	x[19]	.	x	.	x	.	.
Convolvulus	x	.	.	.	x	.	x	x	.	.	.	.	x	.
Ericameria	.	.	x	x	.	.	x	.	x	.	x	x	.	x
Eriogonum	.	.	x	.	x	x	.	.	x	.	x	x	.	.
Franseria	.	x	.	.	x	.	x	x[19]	.	.	.	x	.	.
Lupinus	.	.	x	.	x	x	.	.	x	.	x	.	.	.
Mesembryanthemum	x	.	.	.	x	.	x	x[19]	.	.	.	x	.	.
Oenothera	.	x	.	.	x	x	.	.	x	x	.	x	.	.
Rhus	.	.	x	.	x	x	.	.	x	x	x	x	.	x

[17] Data gathered from El Segundo, Los Angeles County, and Silver Strand, San Diego County, from September, 1931 to January, 1933.

[18] "x" Denotes presence of the characteristic.

[19] When young.

ANATOMY OF THE LEAF

Of all plant organs the leaf is most responsive to changes in environmental conditions, and in sand dune vegetation leaves have become modified in several different ways. Although much of the sand dunes is xero-mesic rather than xeric, plant responses to the peculiar edaphic conditions are decidedly xeric in character. Many of the leaves bear trichomes; closely placed, unbranched, uniseriate ones predominating. They are especially abundant in Franseria and Lupinus, where they are present on both surfaces. In the Abronias the trichomes are glandular, being more abundant in *A. maritima.* Eriogonum has both glandular and non-glandular sorts. In Rhus only unicellular, unbranched forms of scattered occurrence are present, while in Convolvulus and Mesembryanthemum all types are absent. Atriplex is provided with a thick layer of vesicular trichomes; on many dune species, indeed, the trichomal covering is so heavy as to give the leaf a grayish appearance.

Stomata for the most part are small and relatively few in number per unit of surface. They occur in both epidermal layers in *Abronia maritima, A. umbellata,* Atriplex, Convolvulus, Franseria, Lupinus, and Oenothera, on all sides of the needle-like leaves of Ericameria, and on the three sides of the leaf of Mesembryanthemum while on Eriogonum and Rhus they are found in the abaxial alone. Nine of the eleven species have stomata on all sides of the leaf. Frequently subsidiary cells accompany them, as in Mesembryanthemum.

Cuticle is present on all eleven species, but varies considerably in thickness, Atriplex having the thinnest (0.002 mm.) and the adaxial surface of Rhus having the thickest (0.007 mm.).

Epidermal cells are almost uniform on both adaxial and abaxial surfaces, those of the adaxial usually being slightly larger.

The arrangement of the chlorenchyma is an index of the environmental conditions under which sand dune vegetation exists. In some of the species, as in Eriogonum and Lupinus, the mesophyll is composed largely of palisade. This is advantageous, since a leaf of this type transpires less than one whose mesophyll consists of spongy tissue alone. Other species, as the Abronias and Franseria, have palisade at either side of the leaf, being of the diplophyll type, except that sometimes the spongy mesophyll contains few chloroplasts and becomes in part water-accumulative tissue. In Atriplex the chlorenchyma is removed to the center of the blade, with water accumulative tissue above and below it. In all eleven species the leaf tissues are very compact, the degree of this compactness determining to some extent the transpiration.

One of the most striking features of many of the sand dune plants is the abundance of water accumulative tissue. Its position varies in that it may be distributed throughout the mesophyll, as in *Abronia maritima;* in the center of the mesophyll near the veins, as in Convolvulvus, or it may be peripheral,

as under the epidermal surfaces in Atriplex. When the leaves of some of the species become older, they thicken, and much of this thickening is due to an increase in the amount of water accumulative tissue. This is well shown in *Abronia maritima*, where in some cases the cells which were cholorophyll-bearing in the young leaf become enlarged, the chloroplasts disappear, and the cells become wholly storage in function. Water accumulative tissue occurs in seven of the eleven species, namely, in *Abronia maritima*, *A. umbellata*, Atriplex, Convolvulus, Franseria, Mesembryanthemum, and Oenothera. Eighty per cent of the species investigated by Kienholz (1926) had some form of water storage tissue, while Harshberger (1909) listed 20 per cent of his New Jersey sand-strand species as succulent.

Crystals of various types occur in the mesophyll, the most common form, that of bundles of raphides, being present in *Abronia maritima*, *A. umbellata* and Mesembryanthemum. Acicular crystals are found in Convolvulus and Ericameria and druses in Atriplex, Eriogonum, Franseria and Rhus. No crystals were observed in the leaves of Lupinus during the investigation, and were, therefore, present in ten of the eleven species. Latex was found in Convolvulus, resin in Rhus, and mucilage in Mesembryanthemum. Anthocyanin is of general occurrence in the sand dune plants, although found in the leaves of but four of the species investigated, namely, in Convolvulus, *Abronia umbellata*, Mesembryanthemum and Rhus.

Variation in leaf structure within the same species is most evident in the differing proportions of water accumulative tissue in *Abronia maritima*, Con-

TABLE 10. Summary of structural features of the leaf.[20]

Species	Leaf			Trichomes		Palisade				Sponge		Stomata		Inclusions			
	Microphyll	Succulent	Broad sclerophyll	Both surfaces	Abaxial only	Throughout	All surfaces	Adaxial	Center	Present	None	Both surfaces	Abaxial only	Crystals	Latex	Mucilage	Resin
Abronia maritima	.	x[21]	.	x	.	.	x	.	.	x	.	x	.	x			
Abronia umbellata	.	x	.	x	.	.	x	.	.	x	.	x	.	x	.	.	.
Atriplex	.	x	.	x	.	.	.	.	x	x	.	x	.	x	.	.	.
Convolvulus	.	x	.	.	.	.	x	.	.	x	.	x	.	x	x	.	.
Ericameria	x	.	.	.	.	.	x	.	.	x	.	x	.	x			x
Eriogonum	.	.	.	.	x	.	x	.	.	x	.	.	x	x	.	.	.
Franseria	.	x	.	x	.	.	x	.	.	x	.	x	.	x	.	.	.
Lupinus	.	.	.	x	.	x	.	.	.	.	x	x	.	.	.	.	.
Mesembryanthemum	.	x	.	.	.	.	x	.	.	x	.	x	.	x	.	x	.
Oenothera	.	x	.	x	.	.	.	x	.	x	.	x	.	x	.	.	.
Rhus	.	.	x	.	x	.	.	x	.	x	.	.	x	x	.	.	x

[20]Data gathered from El Segundo, Los Angeles County, and Silver Strand, San Diego County, from September, 1931 to January, 1933.

[21]"x" Denotes the presence of the characteristic.

volvulus, and Franseria, an increase of this tissue occurring when these species grow near the strand. In Rhus the number of palisade layers varies from two to three on the adaxial surface.

ANATOMY OF THE ROOT

There is not so much variability here as in the aerial parts. A large cortical parenchyma, with a tendency toward succulence, is found in *Abronia maritima*, *A. umbellata* and Franseria. Convolvulus and Mesembryanthemum, with fibrous roots, have a cortical parenchyma that is very large in proportion to the stele. In Ericameria, Eriogonum, Lupinus, and Rhus, the stele occupies the major portion of the root.

Pith parenchyma rarely occurs; *Abronia maritima*, however, has a rather large area of it. Franseria has its pith cells lignified, while in Atriplex, Lupinus, Eriogonum, Ericameria, and Rhus, xylem and not pith occupies the center of the root. Ericameria and Rhus have a considerable development of cork.

Sclerenchyma is developed in Eriogonum. Starr (1912) found that roots of sand dune plants are generally sclerenchymatous, with collenchyma in the cortex. In the present investigation both were apparently but little developed.

Anomalous structure, in which there are successive rings of cambium producing vascular bundles separated by parenchyma, was found in *Abronia maritima*, *A. umbellata*, Atriplex and Mesembryanthemum.

Crystals are present, principally in the cortical parenchyma, appearing in their most common form, that of bundles of raphides, in *Abronia maritima*, *A. umbellata*, and Mesembryanthemum. No crystals were found during the

TABLE 11. Summary of structural features of the root.[22]

Species	Fibrous	Woody	Tracheae		Tracheids		Sclerenchyma	Inclusions		
			Numerous	Few	Numerous	Few		Crystals	Latex	Resin
Abronia maritima	.	x[23]	.	x	.	x	.	x	.	.
Abronia umbellata	.	x	.	x	.	x	.	x	.	.
Atriplex	.	x	x	.	x	.	.	.	.	.
Convolvulus	x	.	.	x	.	x	.	.	x	.
Ericameria	.	x	.	x	x	.	.	.	.	x
Eriogonum	.	x	.	x	x	.	x	.	.	.
Franseria	.	x	.	x	x	.	.	.	.	x
Lupinus	.	x	.	x	x	.	.	.	.	.
Mesembryanthemum	x	.	.	x	x	.	.	x	.	.
Oenothera	.	x	x	.	x	.	.	.	.	.
Rhus	.	x	x	.	x	.	.	.	.	x

[22] Data gathered from El Segundo, Los Angeles County, and from Silver Strand, San Diego County, from September, 1931 to January, 1933.

[23] "x" Denotes the presence of the characteristic.

investigation in Atriplex, Convolvulus, Ericameria, Eriogonum, Franseria, Lupinus, Oenothera, and Rhus. Resin is present in Franseria and Rhus and latex in Convolvulus.

CORRELATIONS OF ENVIRONMENTAL CONDITIONS AND VEGETATION

TEMPERATURE AND PRECIPITATION AS AFFECTING ALL THE STATIONS

The temperature of the air in these areas is on the whole uniform and moderate. It seldom drops to the freezing point during winter, but even when this does occur, the point of a killing frost is not reached except at very infrequent intervals (Clements, 1916). A marked feature of the Mediterranean type of climate, which is that generally prevalent in southern California, is the non-accordance of favorable temperatures with the rainy season. The El Segundo dune area lies in the "steppe climate" (BShs—dry climate; steppe; hot type; winter precipitation), and the Silver Strand dune area in his "foggy desert climate" (BWhns—dry climate; desert; hot type; foggy summer; winter precipitation) of the Russell (1931) modification of the Köppen international system. The precipitation is somewhat meager, varying considerably from year to year. Ninety per cent falls in the 6 months from November to the end of April, based on the records of the U. S. Weather Bureau stations at San Diego for the past 81 years and at Los Angeles for the past 54 years. In the 3 months, August to November, preceding this period, there is a small amount of precipitation, about 0.59 inch or 6.0 per cent of the annual total at San Diego, and about 0.83 inch or 5.5 per cent at Los Angeles. As this comes after several rainless months, it is practically unavailable to the vegetation growing in a soil already depleted of water. From December to March, when, owing to the low air and soil temperatures, the metabolism of the plant is reduced, soil moisture is abundant and the evaporating power of the air low. In spring the temperature becomes favorable for metabolism, but as the season advances the soil moisture becomes depleted and evaporation increases. Summer and autumn, therefore, are the unfavorable periods.

The vegetation of the dunes has become modified in different ways to meet these conditions. One group of plants, represented by Mesembryanthemum, grows rapidly in early spring when soil moisture is ample and temperatures are becoming favorable, accumulating water for its slow growth during the summer and the autumn. From monthly measurements of twelve stems, Mesembryanthemum grew approximately 2.5 cm. in length per month from August to November, 1932. This appears to be an excellent rate of growth for the unfavorable period of late summer and autumn. From July to November of that year, the rainfall amounted to but 1.4 inches. The soil

moisture at the roots of these plants at this time was about 0.5 per cent, so small an amount that it was probably unavailable to the plant, even if high osmotic pressure was maintained. Conservation of moisture in the plant is aided by a thick layer of cuticle and by embedded stomata.

The second group of plants is suffrutescent. The herbaceous portions of the stems largely die back during the dry season, as in Oenothera. With lessened shoot system during summer, the plant appears to contain sufficient water even though its roots are not deep enough to attain moist soil. Moisture, such as dew, may be absorbed through its aerial portions.

A third group of plants, the shrubs, such as Lupinus, Ericameria and Rhus, probably do not have so great a water deficit as those in the previous groups, since the shrubs have deeply penetrating root systems extending to moist soil layers at all seasons. In addition to this, each of these species has modifications for lessening water loss. Water, however, is not available so soon to the shrubs as to the shallow-rooted succulents, since the early autumn rains are often light and moisten only the surface layers of the soil.

Evaporation and Other Environmental Influences at Each Station

The severest environmental conditions throughout the year are encountered in the moving dunes, in which location Franseria is most frequently found. The most noticeable features of this environment are the instability of the substratum, the intensity of the light, the high evaporation rates, both higher and lower soil temperatures, less soil moisture, and soil of a coarser texture than in any other dune locality. Franseria, with its fleshy tap-root, can withstand partial covering by sand and can make rapid growth. Of the six stations maintained, the moving dune station consistently showed the highest rates of evaporation, almost twice as much as those at any other station. Here higher wind velocity and greater light intensity prevail. Franseria is modified to meet these adverse environmental conditions. Its habit of growth is low and spreading, serving for sand stabilization. With the succulence of its tap-root, and, in addition, with that of its stems and leaves when the plant is growing near the strand, it accumulates rather more water than is superficially apparent. The surfaces of the leaves and younger stems are covered with trichomes. The crystals, present in most of its tissues, probably aid in the concentrating of the cell sap. In the moving dunes the percentage of soil moisture is very low during the summer months; at a depth of 10 cm. less than 0.5 per cent was found monthly in the period of 6 months from May to November, 1932. The roots of Franseria, while penetrating below 10 cm., lie mainly in a layer of soil that has about 1.0 per cent of moisture. The amount of water available from the soil during the summer

period is probably insufficient for the species.[24] Franseria, no doubt, uses its accumulated water.

Next to the moving dunes, the greatest evaporation rates occur near the strand. Here are located *Abronia maritima*, Atriplex, and occasionally Franseria, all of which hold the sand in small foredunes. The soil hereabouts is somewhat more stable, because it is not yet sufficiently dry to be actively blown about, as is the case in areas more removed from the ocean where moving dunes are found. Light intensity is great. There is probably somewhat less wind affecting vegetation here, since the plants lie close to the ground, and are, besides, seldom elevated by means of sand mounds, as happens farther back. There is not so great fluctuation in soil temperature in this area as at the moving dune station, while the soil moisture is greater during the drier portions of the year. The plants of this environment, with succulence their chief characteristic, are in a location where they are at times subject to a deposition of salt spray. Water accumulative tissue is present in the cortical parenchyma of the stems, and sometimes in the roots, of *Abronia maritima* and Atriplex. *Abronia maritima* develops water accumulative tissue somewhat variously in the mesophyll. The cells of the chlorenchyma become enlarged, some of the chloroplasts disappear as such, and the cells are water accumulative in addition to retaining the photosynthetic function in part. Atriplex has its water accumulative tissue located in definite layers inside of either epidermal surface, a position of this tissue which serves to protect the underlying tissues against excessive light. Both species have their leaf and stem surfaces covered with closely overlapping trichomes, those of Abronia being glandular while those of Atriplex are vesicular.

At a depth of 10.0 cm., soil moisture, calculated on the dry weight of the soil, ranged between 0.25 and 0.51 per cent for the period of greatest dryness, the six months May to November, 1932. At 20 cm. depth, it averaged less than 1.0 per cent, and below the latter depth, where roots of Abronia and Atriplex occur, the percentage varied, but was slightly over 1.00 per cent for most of the period mentioned. The species may be able, through the concentration of their cell sap, to secure water, although the amount available must be small.

Near the strand two succulents, Mesembryanthemum and Convolvulus, are found. Mesembryanthemum, with its fleshy equilateral leaves, is the most succulent species of the dunes. Both plants are of low growth habit, Convolvulus spreading by means of rhizomes and Mesembryanthemum by its prostrate aerial stems which root at the nodes. Leaves of both species are covered with a thick layer of cuticle, and the mesophyll is compact, that of Mesembryanthemum being largely of water accumulative tissue. Stomata are present on both surfaces of Convolvulus and on all three sides of the tri-

[24] Kearney (1904), states that a test of soil at Long Beach, Calif., made in September, showed much less water at the time of examination than is usually the case on the Atlantic coast.

angular leaf of Mesembryanthemum, where their frequency no doubt permits considerable transpiration. In the latter species, however, the stomata are depressed in the epidermal layer and protected by an over-hang of the subsidiary cells. Sclereids in the palisade tissue of Mesembryanthemum prevent collapse when turgor is reduced. Mucilage is present in Mesembryanthemum; latex in Convolvulus.

It was observed that Franseria and *Abronia maritima* just back of the strand were much more succulent with larger and thicker leaves than farther inland. Measurements of 50 leaves of Abronia at Guadalupe, Santa Barbara County, close to the strand, showed an average thickness of 5.5 mm.; farther inland, the average was 2.7 mm. Leaves of Franseria were not only thicker but also less pinnatifid. Both species were thriving in either location, their succulence nearer the strand being probably an indication of more xeric conditions there.

Near the strand in an excavation to a depth of 2.5 feet, which was a few inches below the roots of an *Abronia maritima* specimen, the soil showed a slight saltiness.[25]

Species near the strand do not develop root systems as deep as those in the dune complex. Of the strand plants *Abronia maritima* and Atriplex are not deeply rooted. Farther inland Convolvulus has the rhizome habit with a small development of roots. Still farther inland the plants are deeply rooted, such as the shrubs, Lupinus and Ericameria.

At the dune complex stations at El Segundo, Ericameria (3) and Rhus (4), and at the Silver Strand, Rhus (6), the environmental conditions are more favorable for plant growth than at the three other stations, namely, at El Segundo, moving dune (2), Abronia (1), and at the Silver Strand, Abronia (5). The evaporation at the dune complex stations was less than at the others, the light less intense, and the wind velocity reduced. During most of the period when soil moisture data were obtained the soil of the dune complex stations held a higher percentage of moisture and the soil temperature fluctuated less than at the other stations. The vegetation here, more removed from the ocean than at the other stations, consists largely of shrubs—Ericameria, Lupinus, Eriogonum and Rhus. At station 3 the principal shrubs are Ericameria and Lupinus, the most deeply rooted of all the species investigated. In sites which are partially stabilized the shrubs grow with intervals of several feet between them. The compound leaf of Lupinus has small leaflets which are partly infolded; the leaf in Ericameria is linear and microphyllous. With these reduced leaf areas there are but few stomata. Lupinus bears a close covering of trichomes on both epidermal surfaces. Both the species have cuticle on the epidermises of leaves and young stem, that on the leaves of Ericameria being especially heavy.

[25] Kearney (1904), states that borings at Long Beach, Calif., showed a quite uniform salt content for the first 3 dm. of soil, ranging from 0.12 to 0.15 per cent of water soluble salts.

Environmental conditions are most favorable at the Rhus stations at El Segundo and at the Silver Strand, as compared with the other four stations. Evaporation is consistently less throughout the year at the Silver Strand, with much reduced evaporation rates during the summer months. At El Segundo, during periods when evaporation increases, the increase is less at the Rhus station than at the other three stations, and when it decreases at all stations, it usually decreases but slightly at the Rhus station. In other words, there is less fluctuation at the Rhus station than at the other locations.

Cuticle, especially thick on the adaxial surface, covers the leaves and young stems of Rhus as it does that of Eriogonum, sometimes associated with Rhus. Stomata are present only on the abaxial surfaces, while in Eriogonum this surface is covered by a layer of overlapping trichomes, forming a felt-like covering which cuts down the circulation of air over the leaf and prevents rapid evaporation through the stomata. The leaves of Eriogonum have dense palisade tissue, while in Rhus with two to four rows of palisade, stiffness is supplied by sclerenchyma and collenchyma.

SUMMARY

1. An autecological investigation of the gross morphology and internal anatomy of eleven representative species of the coastal sand dunes of southern California was conducted. Data were obtained of certain important environmental conditions under which the southern California sand dune vegetation grows. An attempt was made to correlate the characteristics and modifications of the species with these conditions of the environment.

2. The southern California coastal sand dunes differ from many such dunes in other areas in that no plants, even if tree species, attain the tree form, the climax appearing to be one of shrubs.

3. Grasses, which are usually a conspicuous feature of sand dune vegetation elsewhere, are scarce in southern California dunes. Aside from *Ammophila arenaria* (L.) Link, which has been introduced, there are no true dune grasses, in as much as those present are typically ruderal or are saline species, such as *Monanthochloe littoralis* Engelm. and *Distichlis spicata* (L.) Greene, which became established in saline locations and upon which sand later accumulated.

4. In plants growing under the xeric dune conditions various structural modifications have developed, such as a sclerophyll type of stiff structure with compact tissues, and a succulent type with a high percentage of water.

5. Differences in the species comprise not only modifications due to variations in the environmental conditions, such as change in the amount of succulence, but also genetic variations, such as growth-form.

6. Plants, such as Franseria, growing in moving dunes and also in more or less level sand areas where the evaporation rates are greatest, exhibit a

low, mostly prostrate growth-form, small leaves, succulent tissue, and a heavy covering of overlapping trichomes on the leaves and stems, giving them a silvery-gray appearance. Their root systems are comparatively shallow.

7. Transition between the more advanced stages of dune vegetation and the chaparral of the inland hills may be indicated by the presence of Rhus. Where this plant occurs are located the more mesic areas of the dunes, in which the evaporation rates are the lowest. It is a shrub, with heavily cutinized, stiff, leathery leaves, with very few trichomes and no succulent tissue.

8. Some species, as *Abronia maritima* and Franseria, when growing near the ocean, bear fleshy leaves, while farther inland the leaves of these plants are less fleshy.

9. Stomatal transpiration appears to be unchecked by any special device in the eleven species, with the possible exception of trichomes.

10. The sand dune plants have a water deficit, at least during certain times of the year, as is shown by their ability to absorb water through their uninjured leaves and stems as they grow in their natural environment.

11. In the littoral of southern California the uniform climate, the rainy season, and, at other times of the year, the moisture from low and high fogs with considerable deposition of dew, make for a fairly low evaporation rate and keep both the air and the soil temperatures favorable for growth during most of the year.

12. The roots are for the most part of normal anatomical structure, being either typically woody as in Eriogonum, Ericameria, Lupinus, and Rhus, or with a somewhat fleshy cortical layer, as in Franseria, Convolvulus, and Oenothera. Anomalous structure is a typical feature of *Abronia maritima, A. umbellata*, Mesembryanthemum and Atriplex.

13. The stems are either of a typical woody type, as in Lupinus, Eriogonum, Ericameria, and Rhus, or succulent, as in *Abronia maritima, A. umbellata*, Convolvulus, Atriplex and Mesembryanthemum.

14. The most pronounced modifications appear in the leaves, ranging from very succulent types, such as Mesembryanthemum and Abronia, to broad sclerophyll, as in Rhus. There are differences in size among the species, though such differences are relatively small. There also occur differences in shape from equilateral to flat and lobed.

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EXPLANATION OF PLATES

All sectional drawings are on a one foot scale.
(A) Vertical section of plant.
(a) Surface of the ground.
(B) Horizontal view of roots.

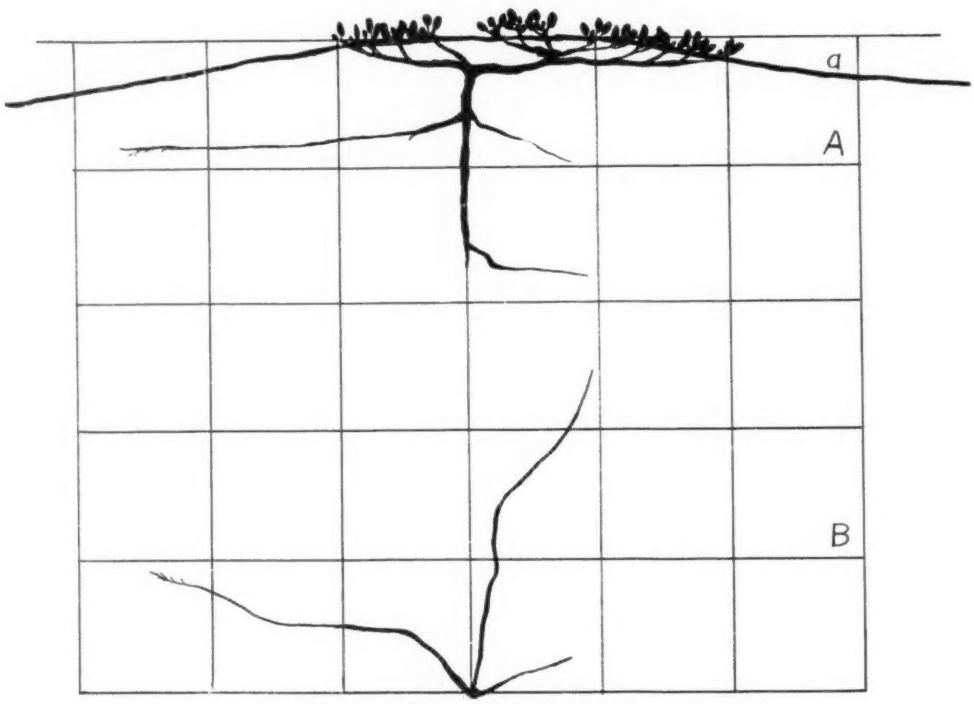

Plate 1. *Abronia maritima* Nutt.

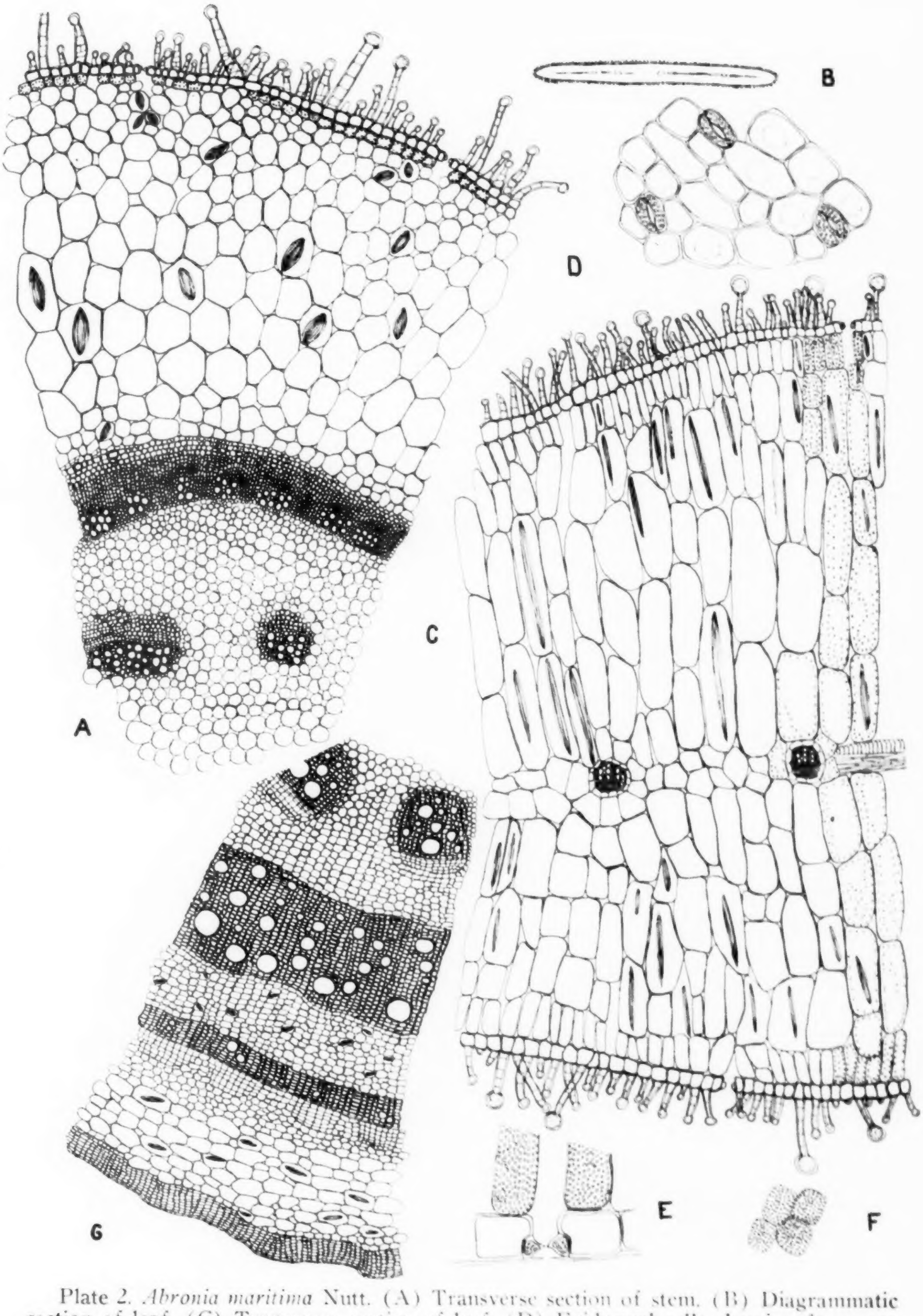

Plate 2. *Abronia maritima* Nutt. (A) Transverse section of stem. (B) Diagrammatic section of leaf. (C) Transverse section of leaf. (D) Epidermal cells showing frequency of stomata. Adaxial and abaxial surfaces are approximately alike. The faint circular lines in some of the cells are the bases of trichomes. (E) Transverse section through epidermal layer showing stoma. (F) Four palisade cells, top view, showing the close placement of chloroplasts. (G) Transverse section of root.

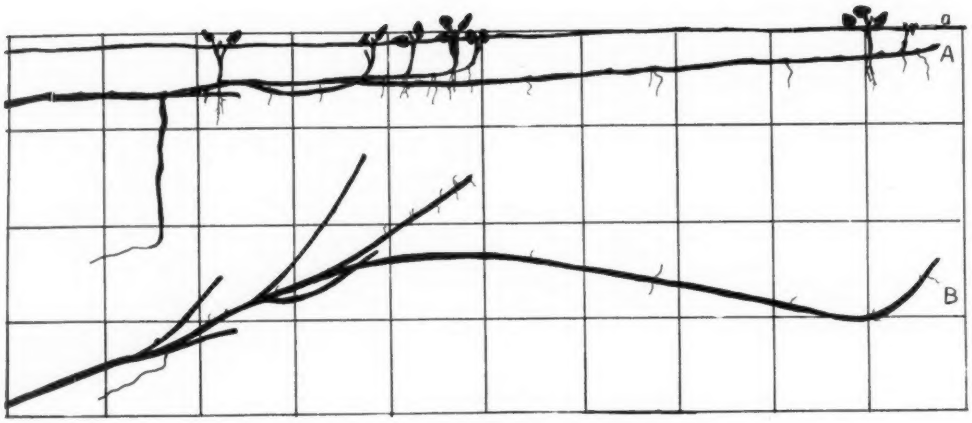

Plate 3. *Convolvulus soldanella* L.

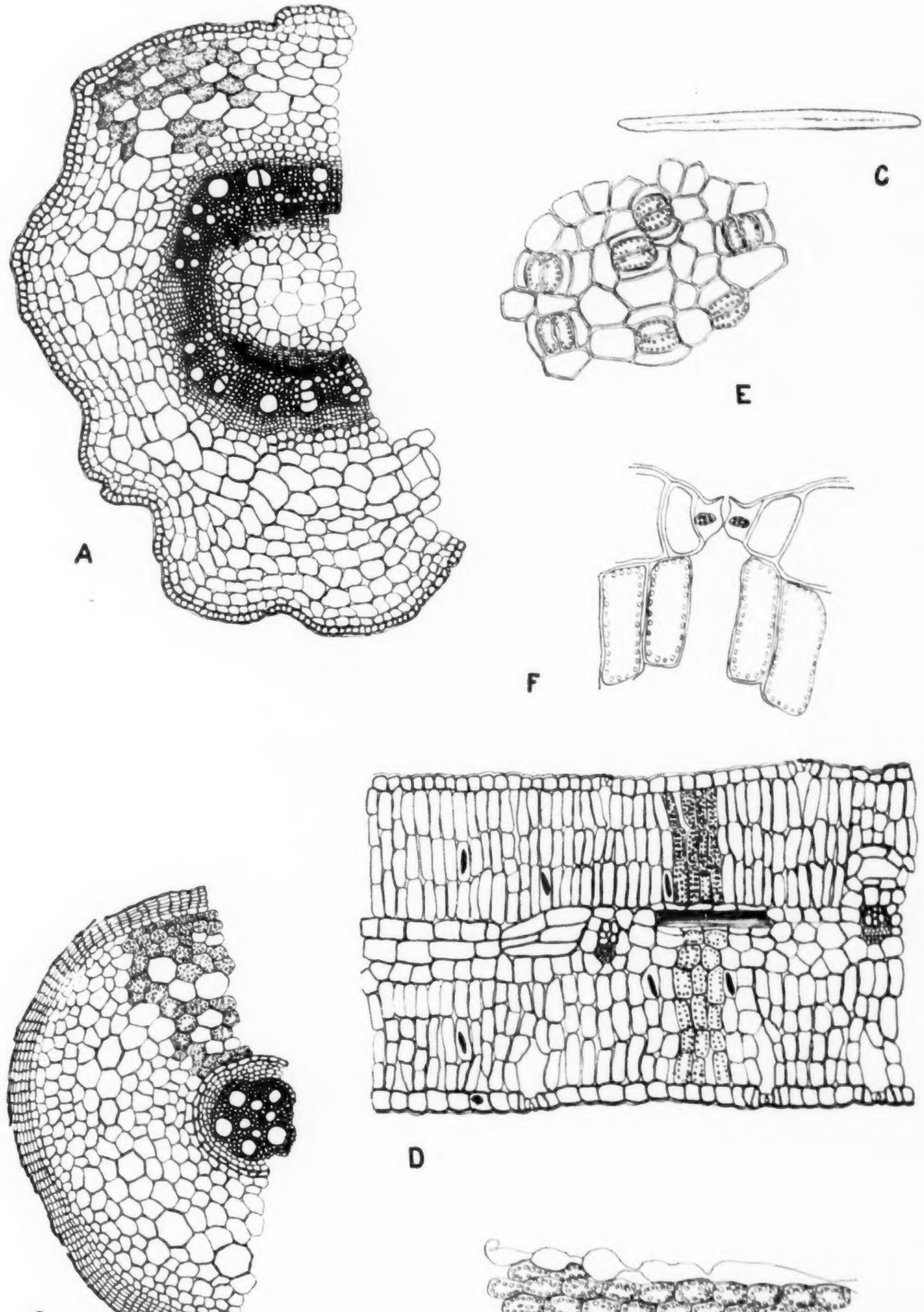

Plate 4. *Convolvulus soldanella* L. (A) Transverse section of stem, indicating in one portion the relative abundance of starch grains. (B) Longitudinal section through stem, showing the laticiferous ducts and adjacent cells. (C) Diagrammatic transverse section of leaf. (D) Transverse section of leaf. (E) Adaxial epidermis, showing frequency of stomata. (F) Transverse section through epidermal layer showing stoma. (G) Transverse section of root, indicating in one portion the relative abundance of starch grains.

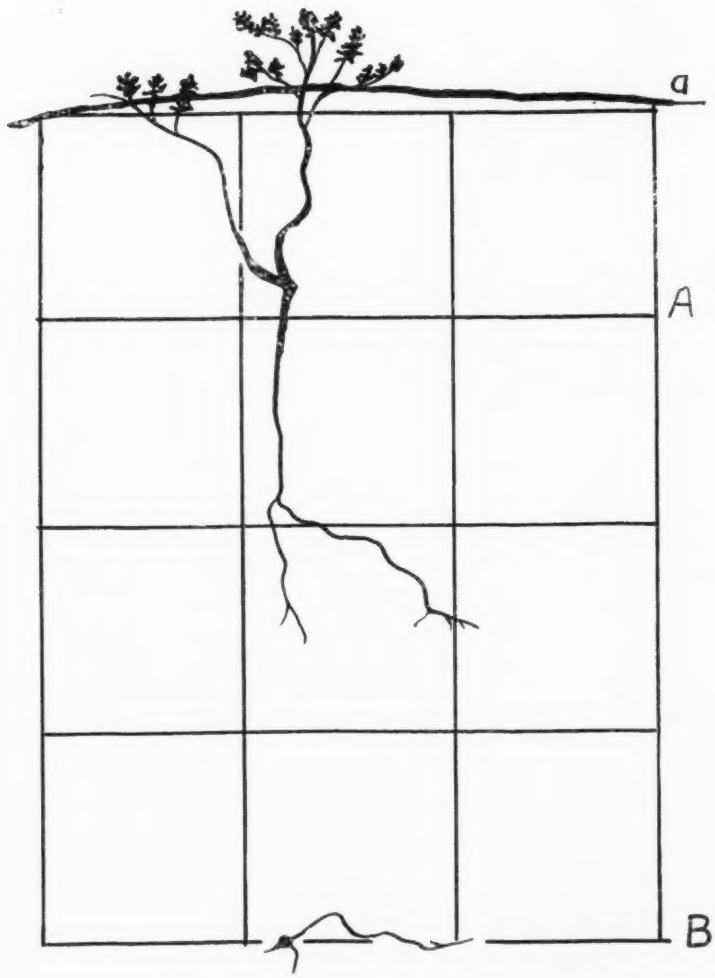

Plate 5. *Atriplex leucophylla* Dietr.

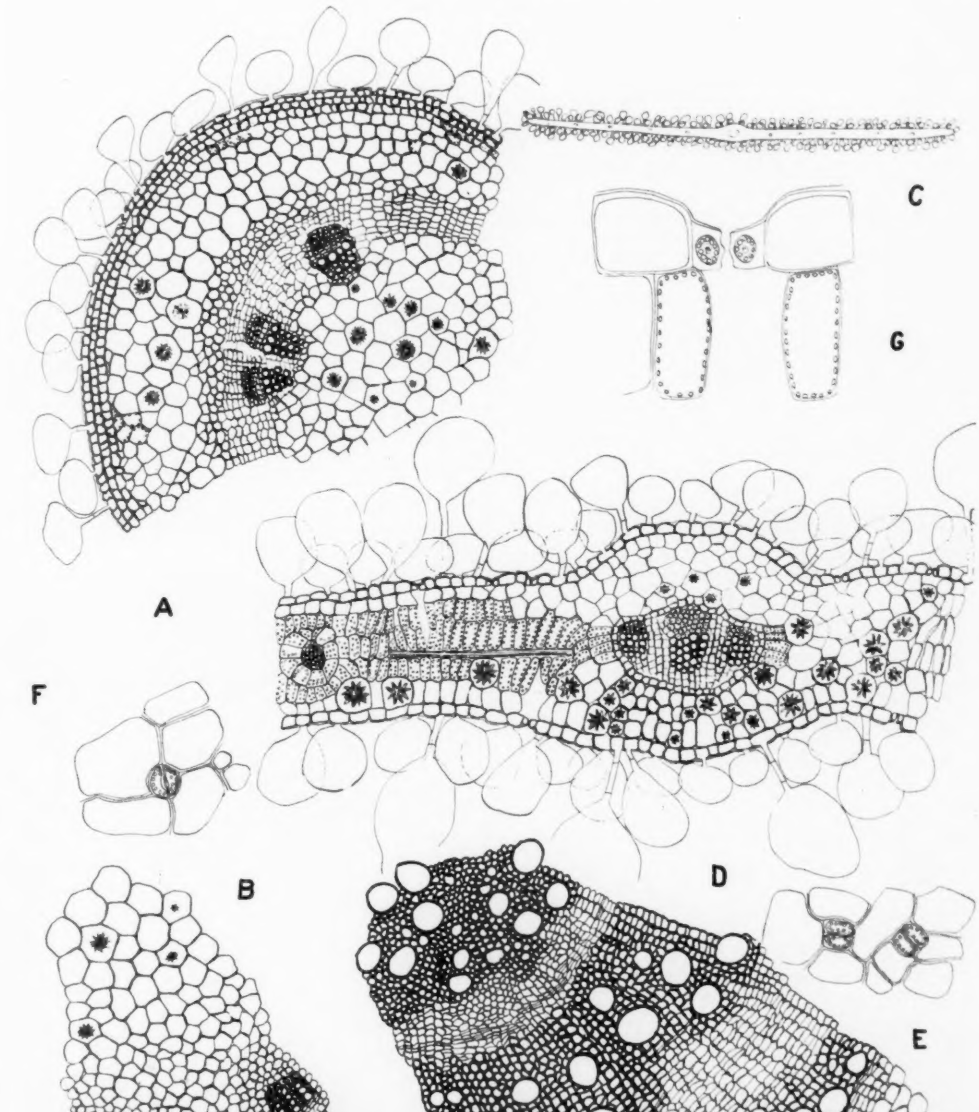

Plate 6. *Atriplex leucophylla* Dietr. (A) Transverse section of young stem. (B) Transverse section of older stem. (C) Diagrammatic transverse section of leaf. (D) Transverse section of leaf. (E) Abaxial surface of leaf, showing stomata. (F) Adaxial surface of leaf, showing stoma. (G) Transverse section through stoma. (H) Transverse section of root.

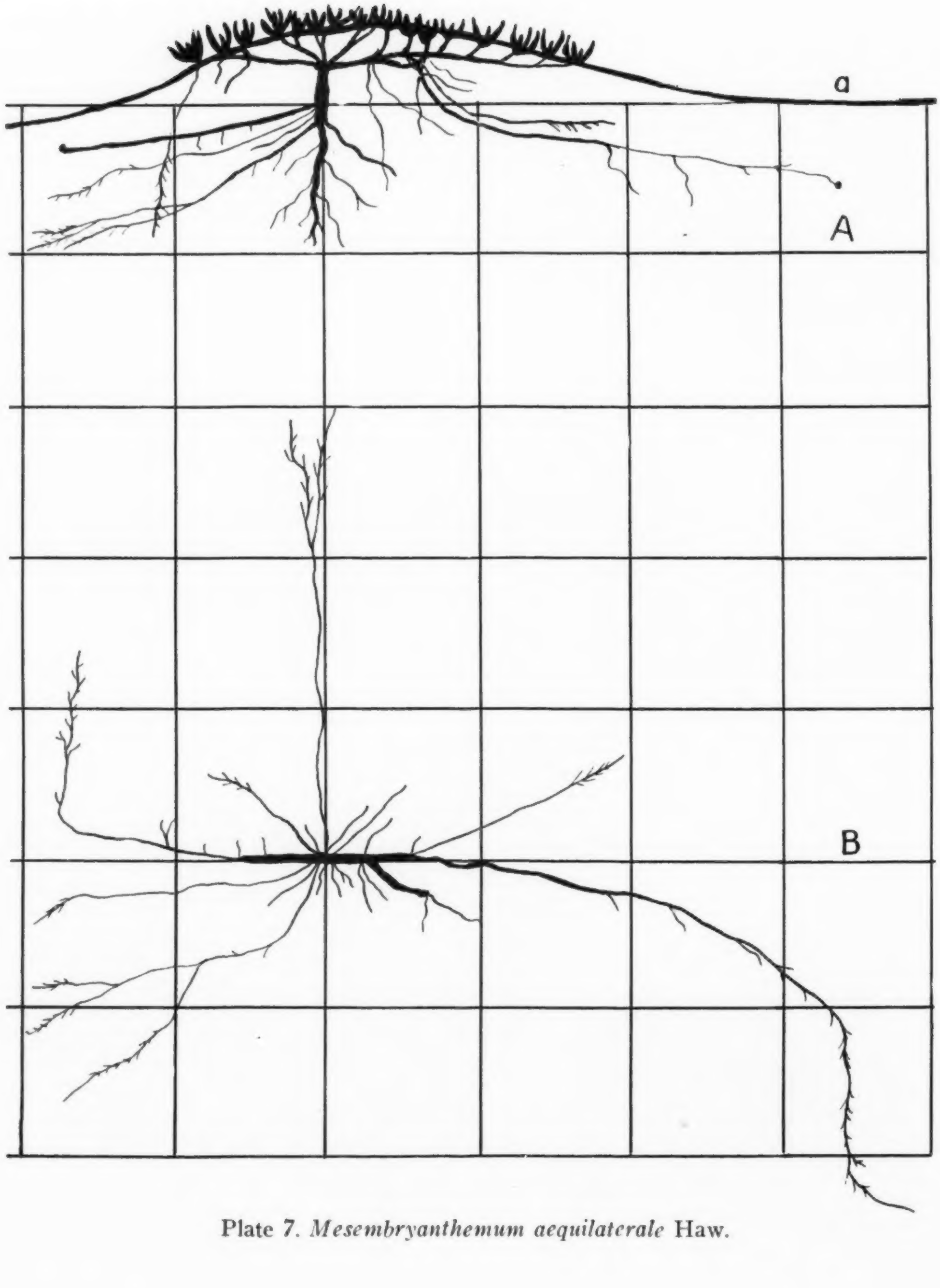

Plate 7. *Mesembryanthemum aequilaterale* Haw.

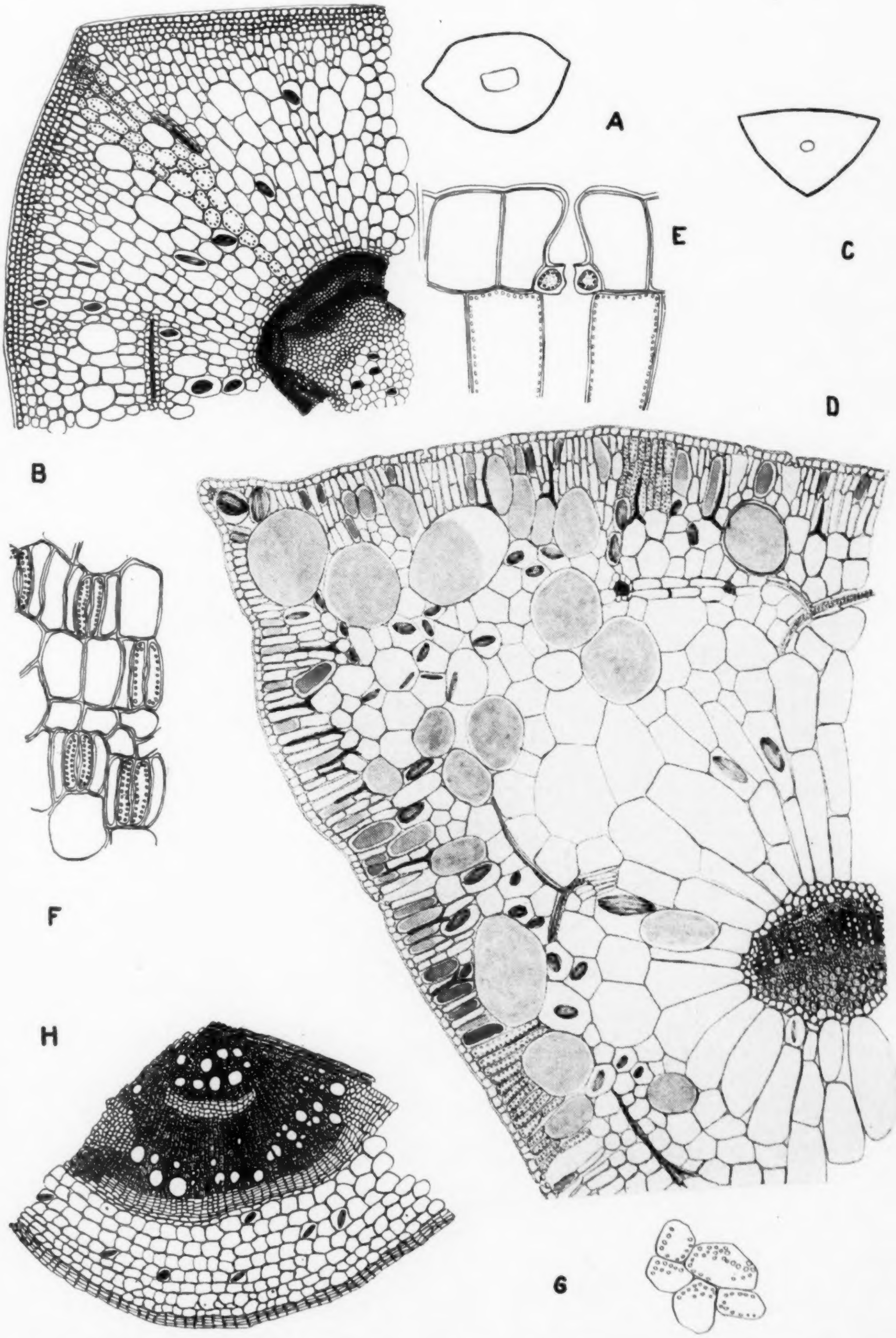

Plate 8. *Mesembryanthemum aequilaterale* Haw. (A) Diagrammatic transverse section of stem. (B) Transverse section of stem. (C) Diagrammatic transverse section of leaf. (D) Transverse section of leaf. (E) Transverse section through the epidermal layer, showing stoma. (F) Epidermal cells, showing frequency of stomata. (G) Cells of leaf, showing starch grains. (H) Transverse section of root.

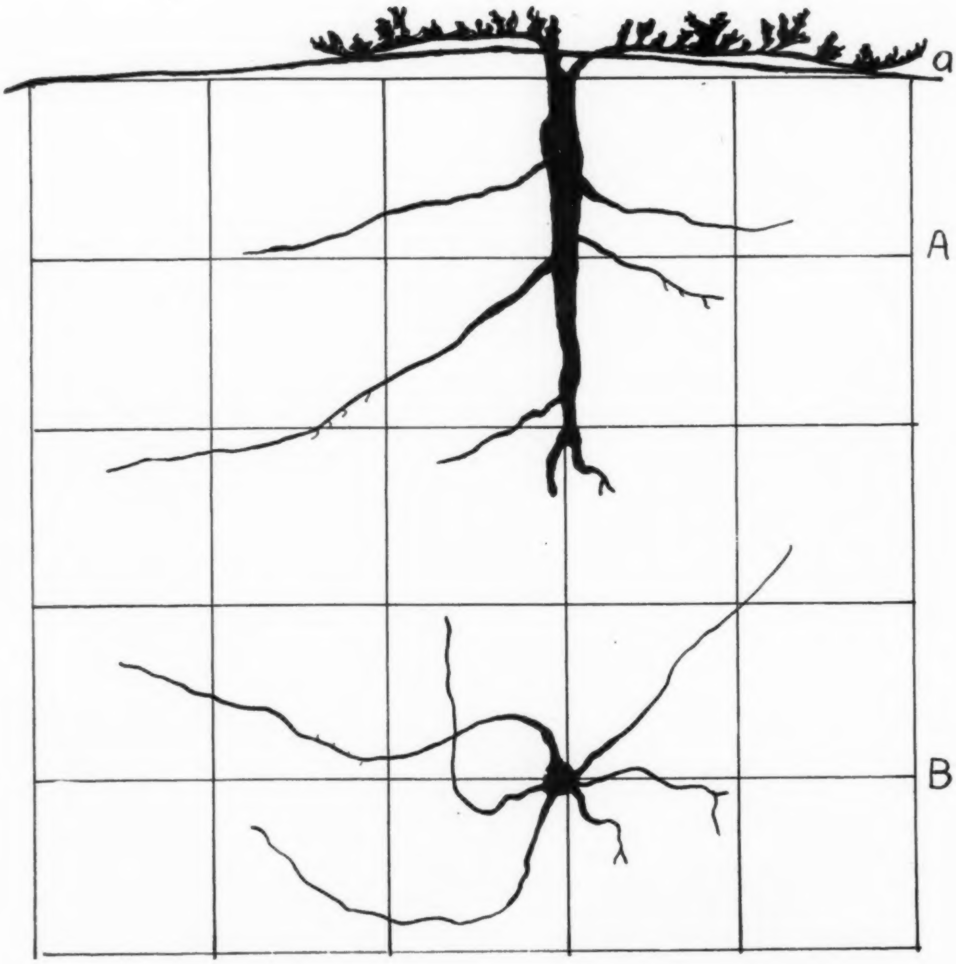

Plate 9. *Franseria bipinnatifida* Nutt.

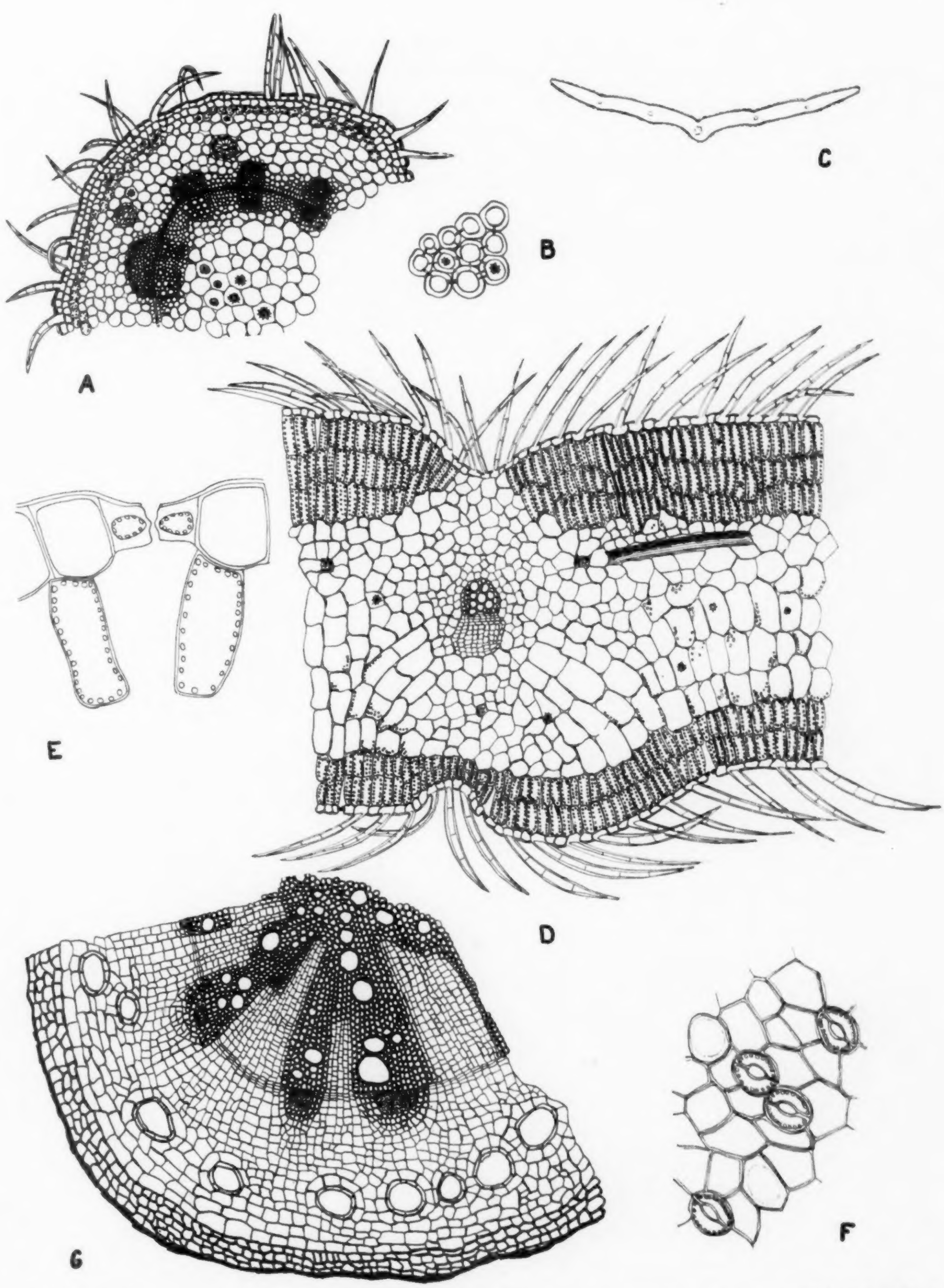

Plate 10. *Franseria bipinnatifida* Nutt. (A) Transverse section of stem. (B) Lignified pith cells, in the center of older stem. (C) Diagrammatic transverse section of leaf. (D) Transverse section of leaf at the midrib. (E) Transverse section through the epidermal layer, showing stoma. (F) Epidermal cells with stomata on abaxial surface. The two epidermal surfaces are approximately alike. The faint circular lines in some of the cells are the bases of trichomes. (G) Transverse section of root.

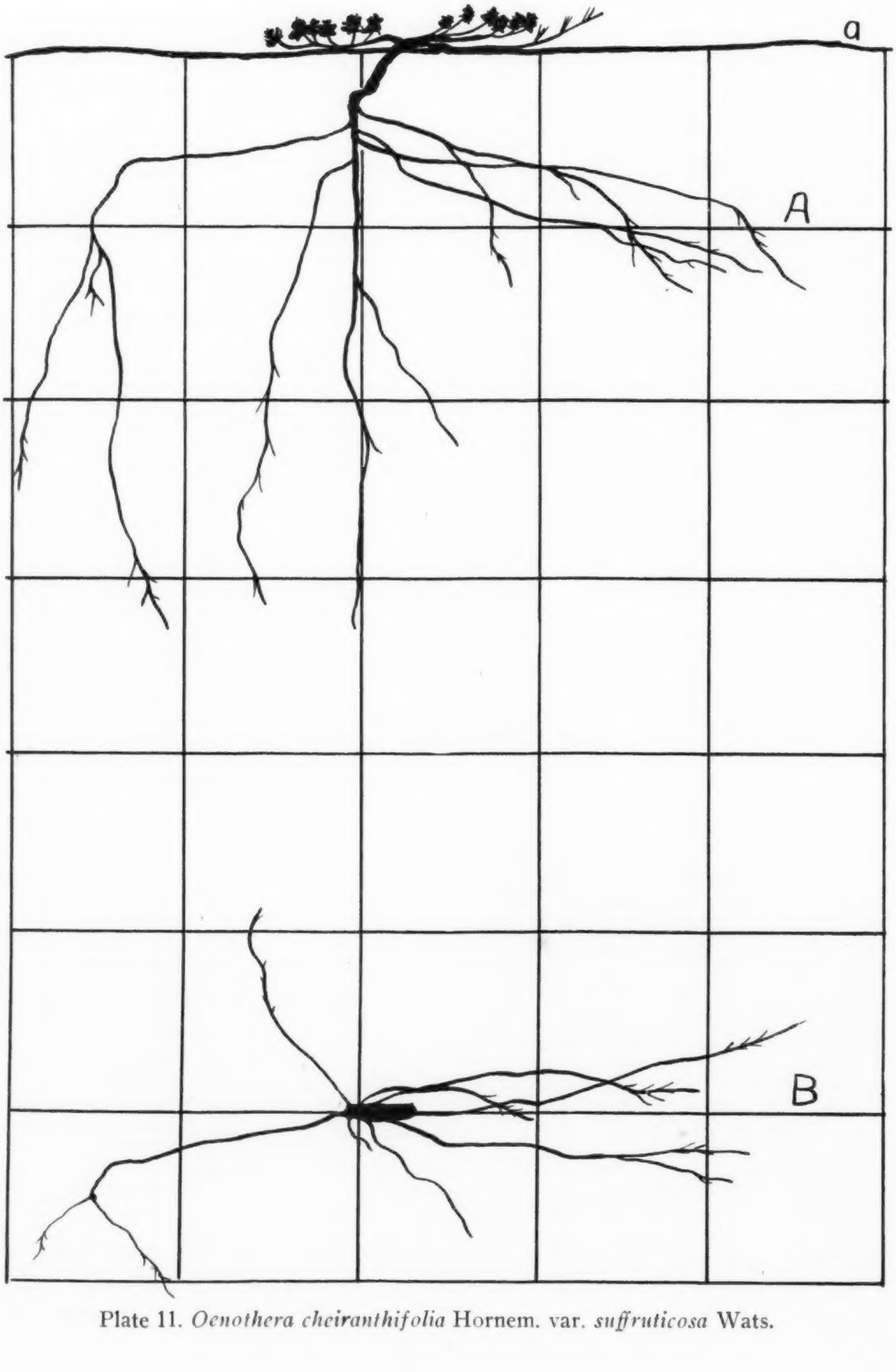

Plate 11. *Oenothera cheiranthifolia* Hornem. var. *suffruticosa* Wats.

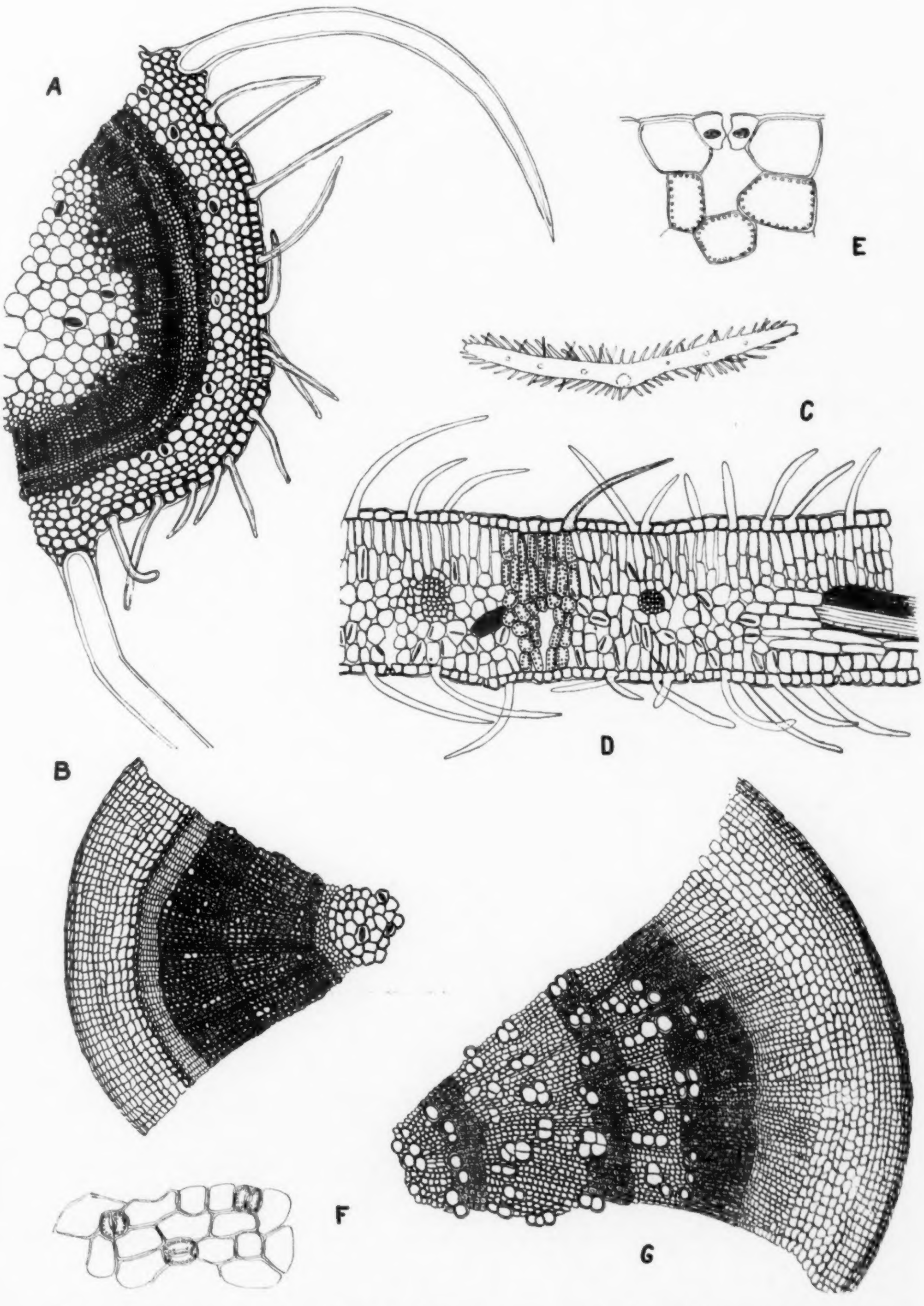

Plate 12. *Oenothera cheiranthifolia* Hornem. var. *suffruticosa* Wats. (A) Transverse section of young stem. (B) Transverse section of older stem. (C) Diagrammatic transverse section of leaf. (D) Transverse section of leaf. (E) Transverse section through epidermal layer, showing stoma. (F) Epidermal cells, showing stomata. (G) Transverse section of root.

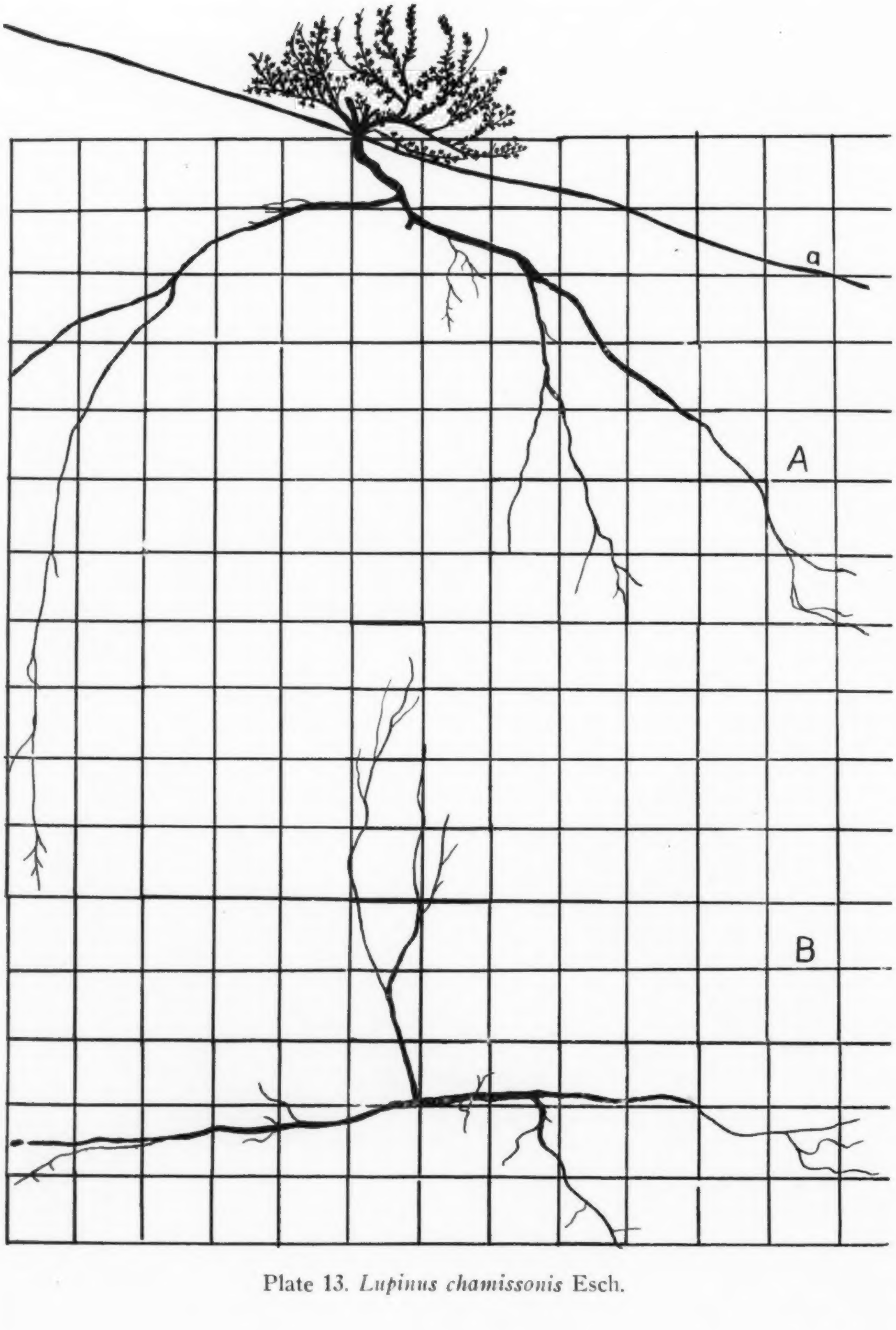

Plate 13. *Lupinus chamissonis* Esch.

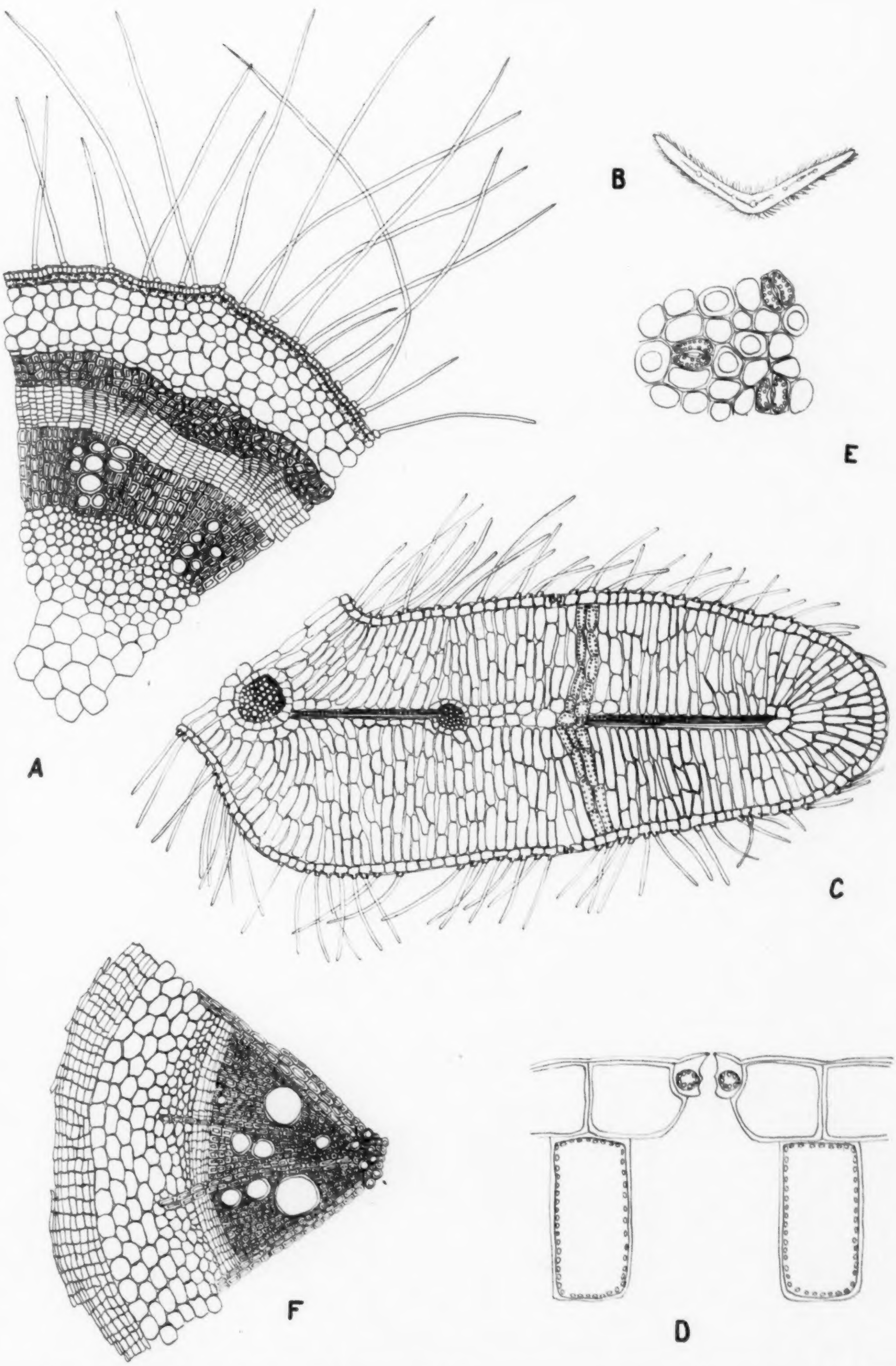

Plate 14. *Lupinus chamissonis* Esch. (A) Transverse section of young stem. (B) Diagrammatic transverse section through leaflet (C) Transverse section of leaflet. (D) Transverse section through epidermal layer, showing stoma. (E) Epidermal cells, showing frequency of stomata. Adaxial and abaxial surfaces are approximately alike. (F) Transverse section of root.

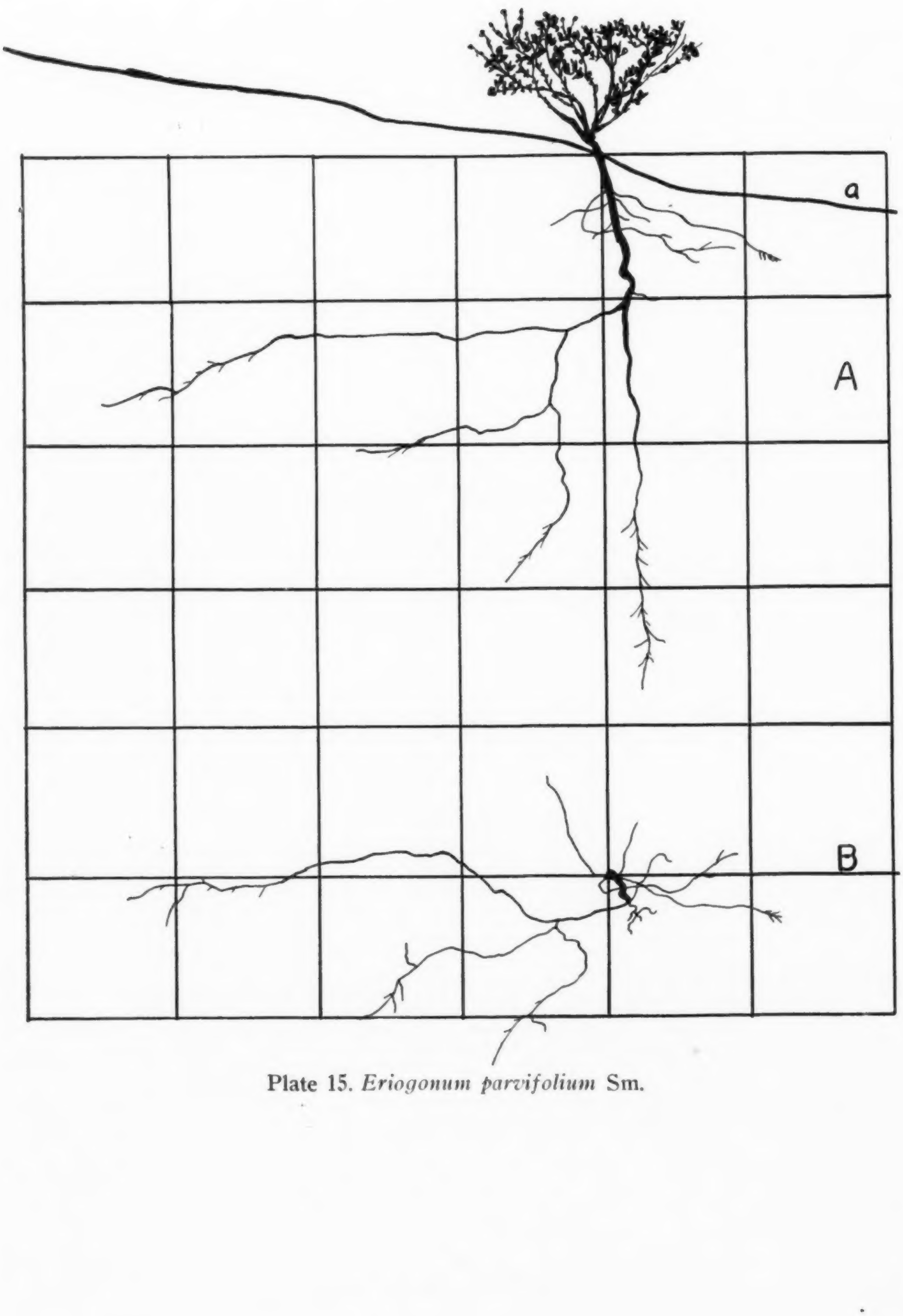

Plate 15. *Eriogonum parvifolium* Sm.

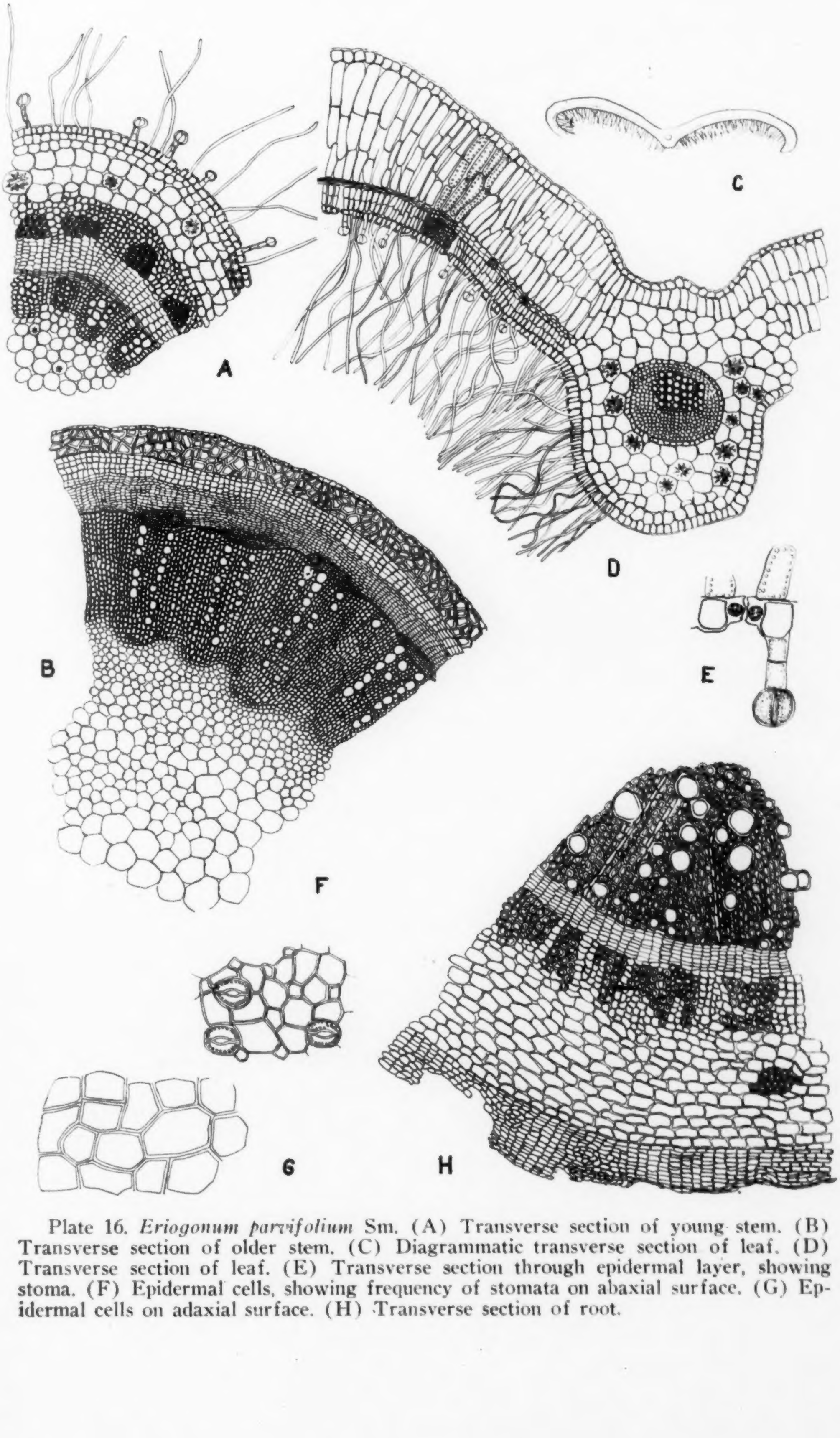

Plate 16. *Eriogonum parvifolium* Sm. (A) Transverse section of young stem. (B) Transverse section of older stem. (C) Diagrammatic transverse section of leaf. (D) Transverse section of leaf. (E) Transverse section through epidermal layer, showing stoma. (F) Epidermal cells, showing frequency of stomata on abaxial surface. (G) Epidermal cells on adaxial surface. (H) Transverse section of root.

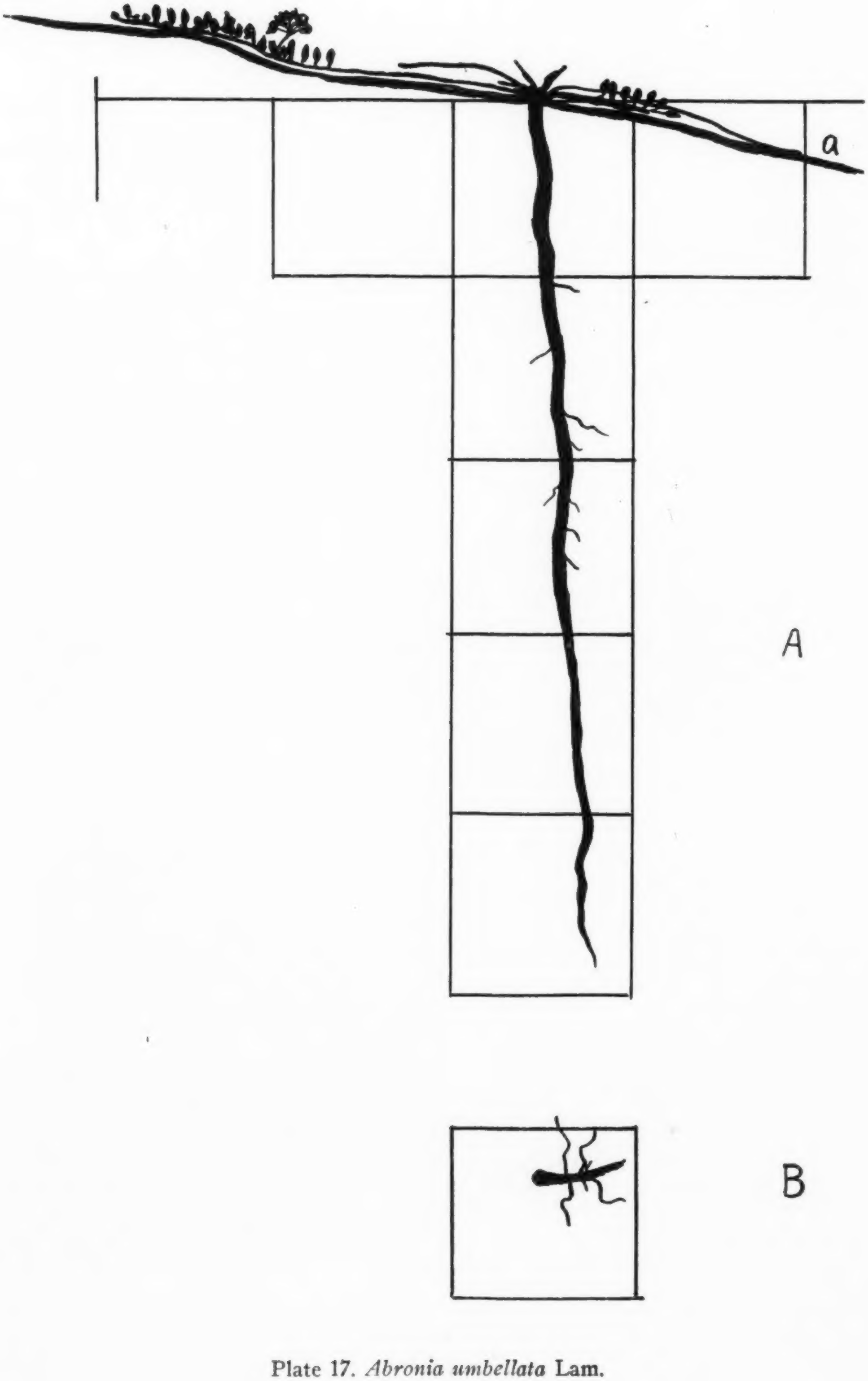

Plate 17. *Abronia umbellata* Lam.

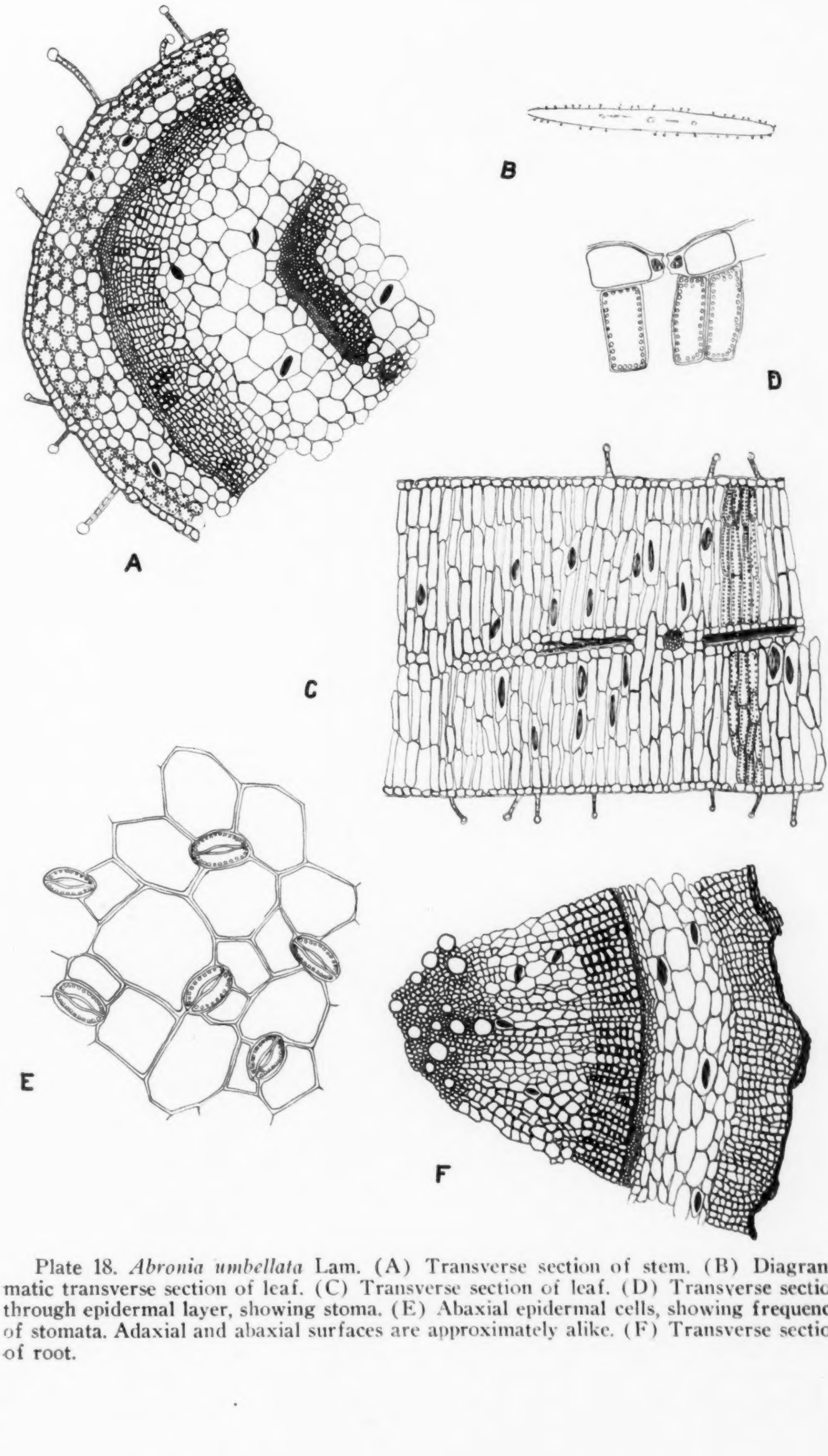

Plate 18. *Abronia umbellata* Lam. (A) Transverse section of stem. (B) Diagrammatic transverse section of leaf. (C) Transverse section of leaf. (D) Transverse section through epidermal layer, showing stoma. (E) Abaxial epidermal cells, showing frequency of stomata. Adaxial and abaxial surfaces are approximately alike. (F) Transverse section of root.

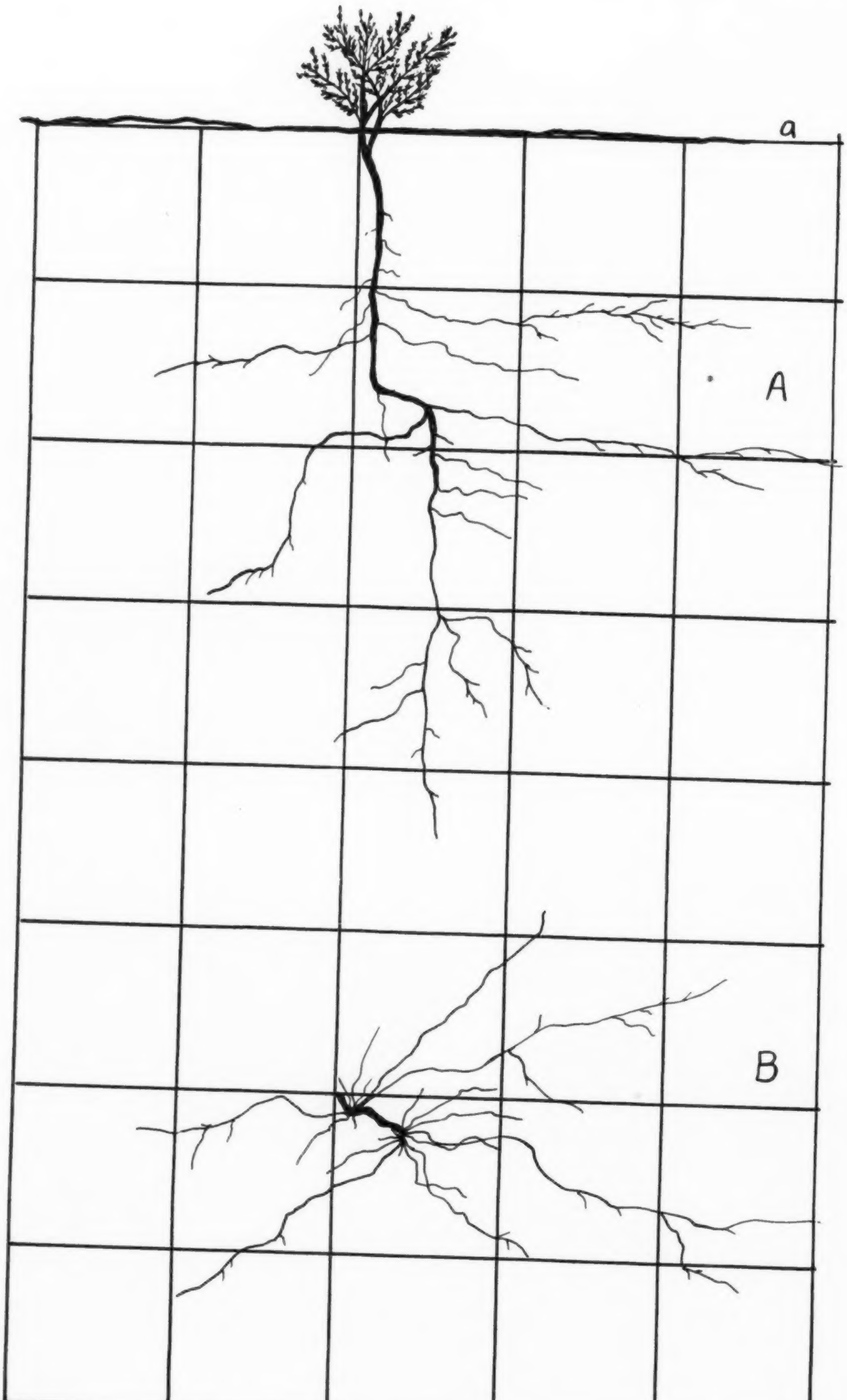

Plate 19. *Ericameria ericoides* (Less.) Jepson.

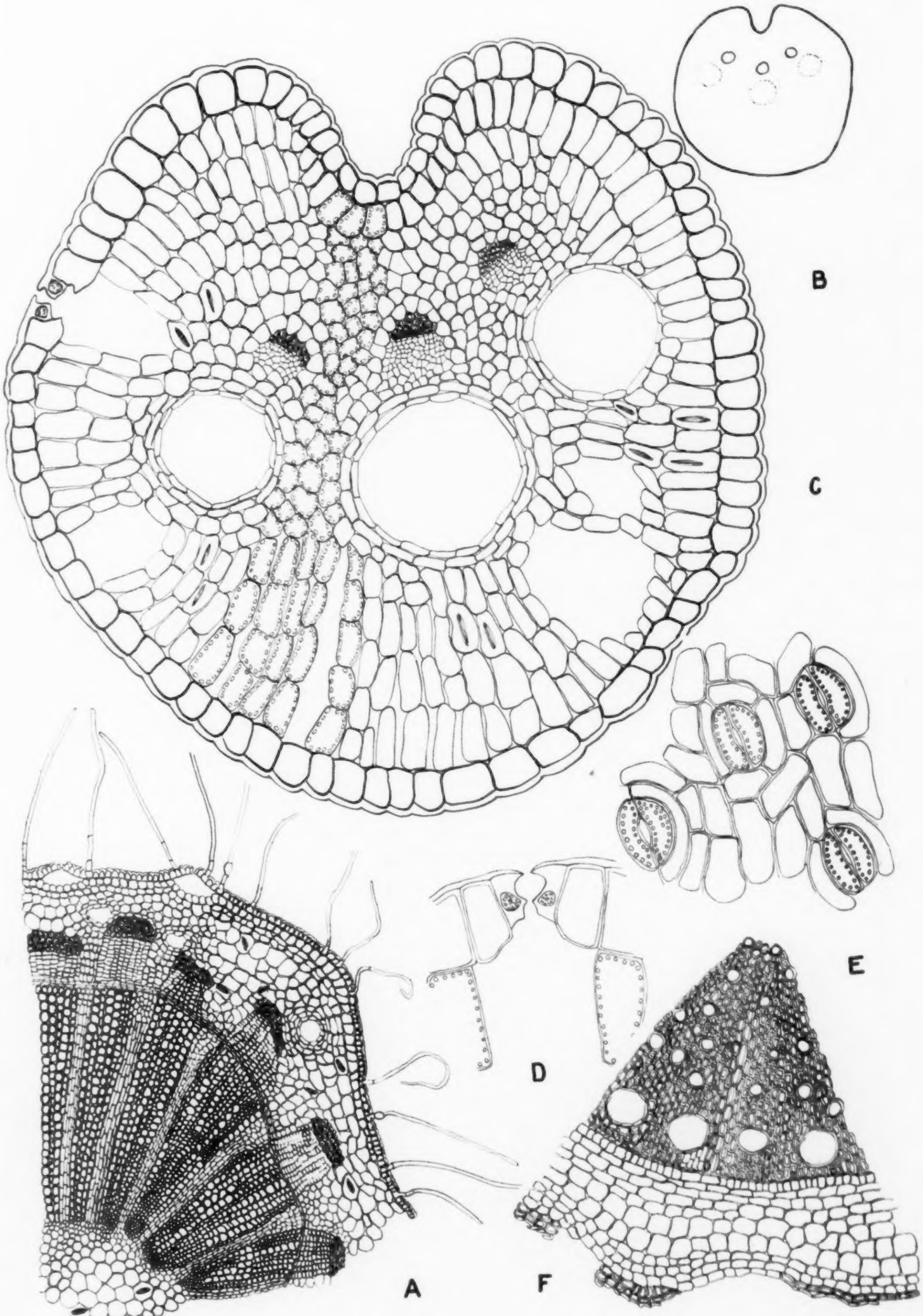

Plate 20. *Ericameria ericoides* (Less.) Jepson. (A) Transverse section of stem. (B) Diagrammatic transverse section of leaf. (C) Transverse section of leaf cut through one stoma. They are present, however, on all sides of the leaf. (D) Transverse section through epidermal layer, showing stoma. (E) Epidermal cells, showing frequency of stomata. All sides of the leaf have about the same stomatal frequency. (F) Transverse section of root.

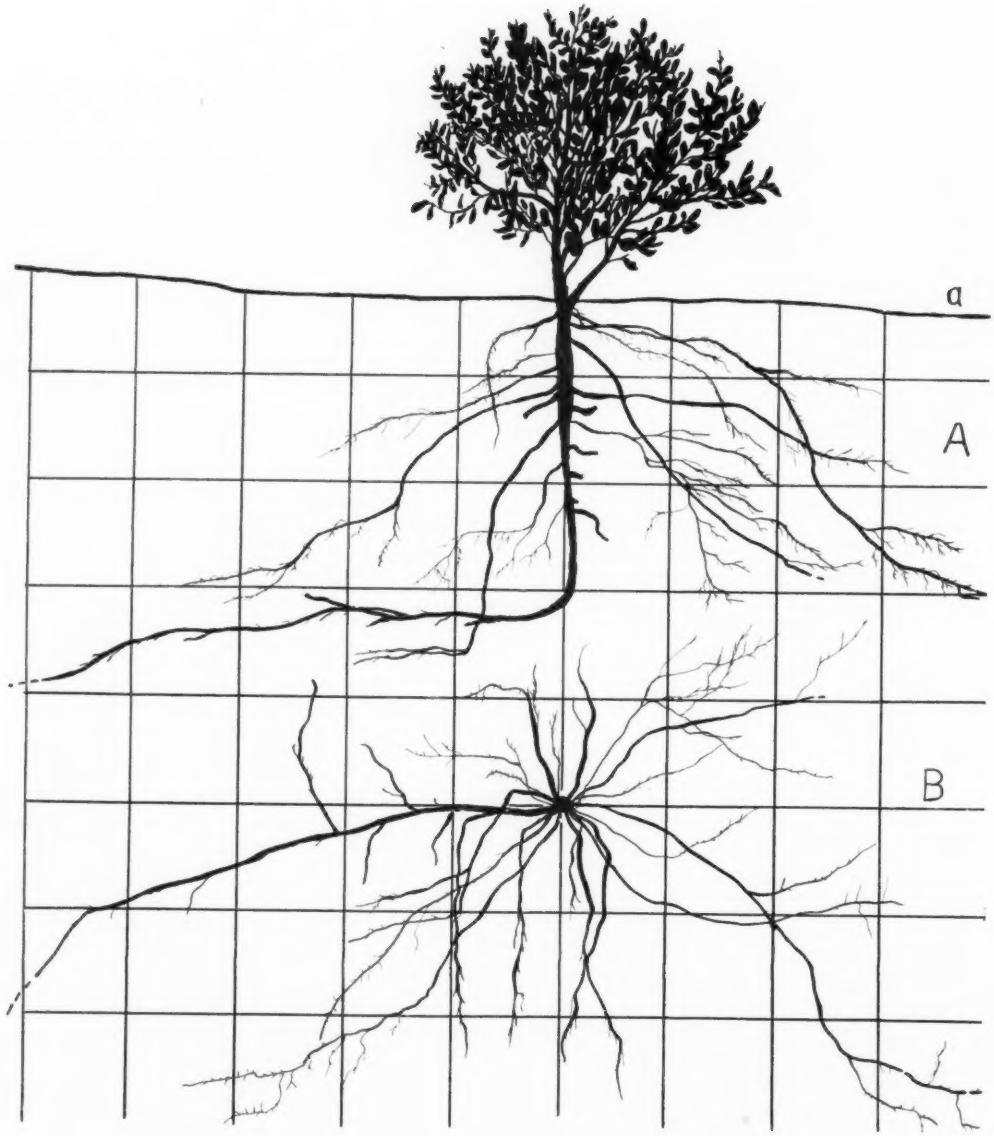

Plate 21. *Rhus integrifolia* B. & W.

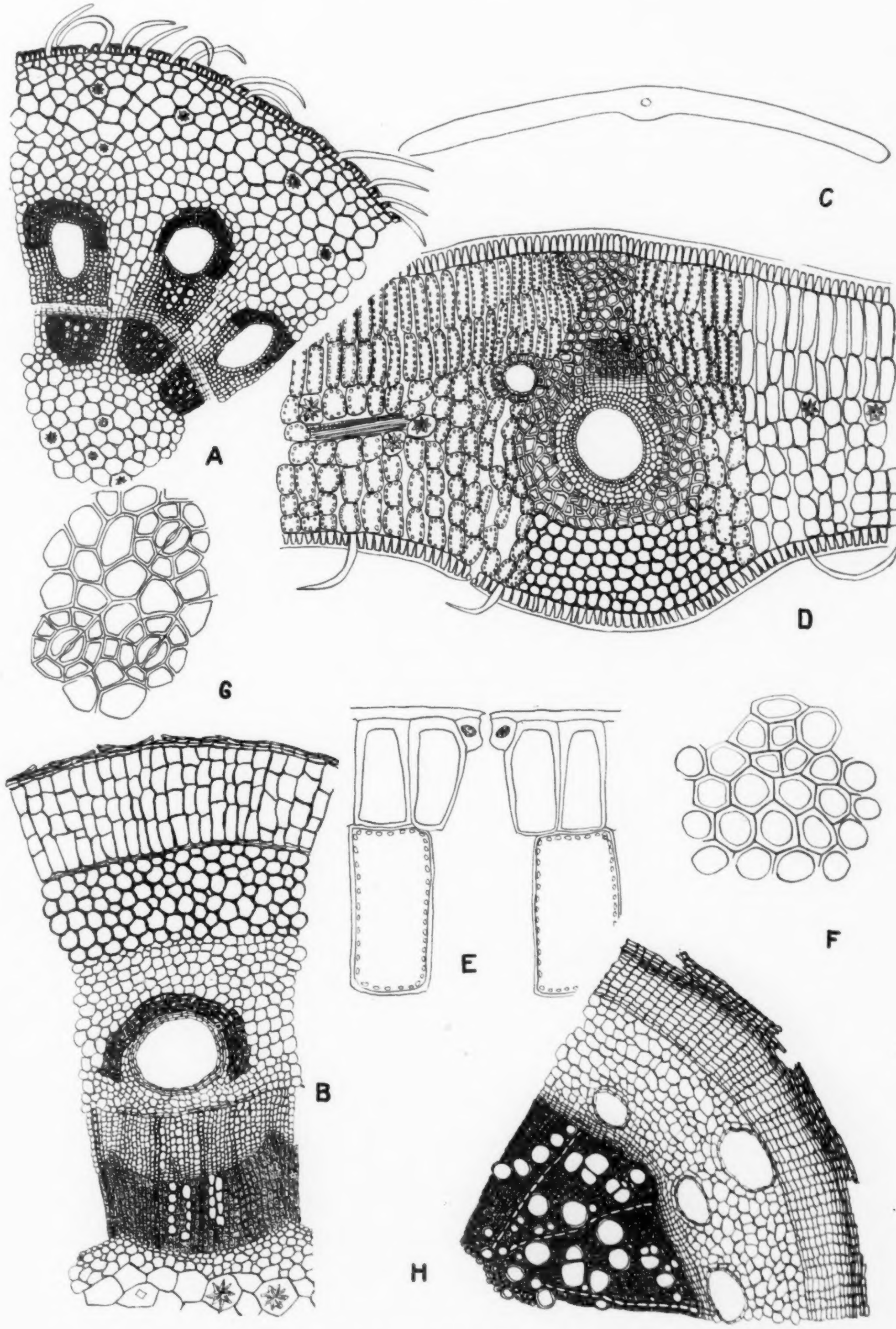

Plate 22. *Rhus integrifolia* B. & W. (A) Transverse section of young stem. (B) Transverse section of older stem, showing one resin-canal surrounded by arc of sclerenchyma. (C) Diagrammatic transverse section of leaf. (D) Transverse section of leaf. (E) Transverse section through the epidermal layer, showing stoma. (F) Adaxial surface, showing epidermal cells. (G) Abaxial surface, showing epidermal cells and stomata. (H) Transverse section of root.

FORESTS OF THE ILLINOIAN TILL PLAIN OF SOUTHWESTERN OHIO

By

E. Lucy Braun

University of Cincinnati

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FORESTS OF THE ILLINOIAN TILL PLAIN OF SOUTHWESTERN OHIO

I. INTRODUCTION

The Illinoian till plain in southwestern Ohio contrasts with adjacent areas in certain vegetational, topographic, and soil features. For this reason it may be considered as a distinct region. Vegetationally, it is a part of the eastern deciduous forest formation, but is delimited by differences in developmental stages and in forest composition from surrounding areas. Swamp forests in which pin oak, sweet gum, white elm, and red maple are important, prevail or did before man cleared and otherwise changed the environment. Common mesophytic trees of the adjacent Cincinnati region and of smaller maturely dissected areas in the general till plain region, as sugar maple, tulip, sweet buckeye, and basswood are absent or rare on the Illinoian till plain in Ohio.

The accompanying map (Fig. 1) shows the glacial boundaries, the area of till plains considered in this paper, and the location of the "Flats" in Indiana. No term has been used to designate this plain in Ohio, though various local names including "flats" are in common use.

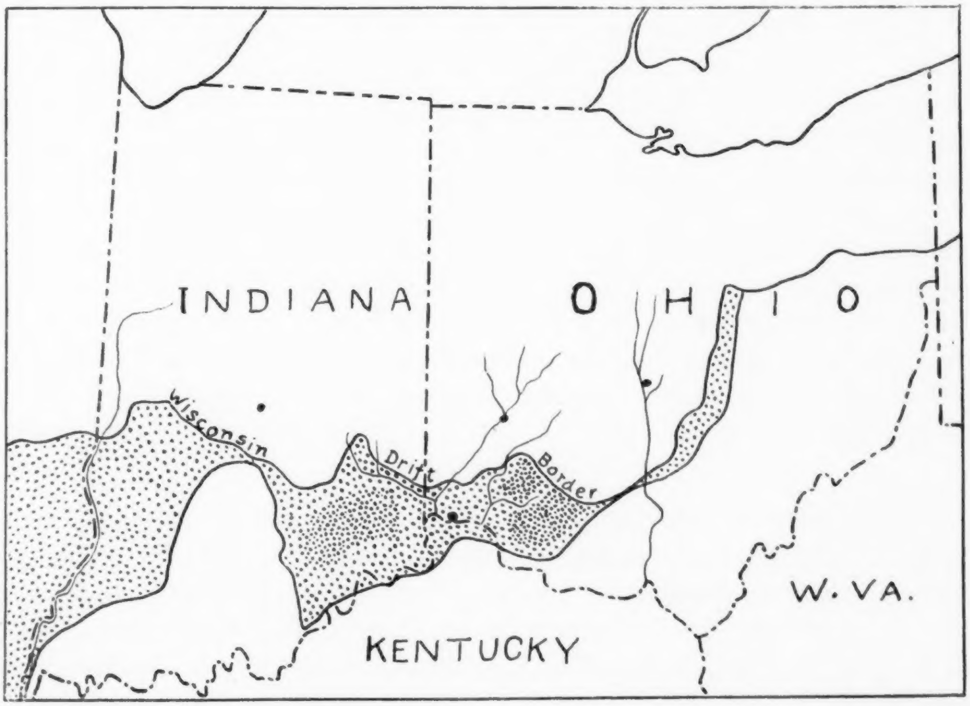

FIG. 1. Map of Ohio and Indiana showing Illinoian drift area (stippled) and boundary of Wisconsin drift. Location of "Flats" of Indiana and of undissected till plain of southwestern Ohio indicated by closer stippling. (After Leverett, 1902, 1915, and Deam, 1921.)

The great southward extending lobe of Illinoian glacial deposits in Ohio and Indiana is divisible into three parts: an eastern section, the Illinoian till plain under consideration in this paper; a central strongly dissected section lying for the most part between the Little Miami and Whitewater rivers (approximately the Cincinnati region); and a flat western section, the "Flats" of Indiana, very similar to the eastern section. Local communities on the occasional small flats in the central dissected section are ecologically a part of the vegetation of the till plains (Braun, 1916). In the "Flats" of southeastern Indiana are large areas of forest comparable to those of the Ohio till plain.

Elsewhere, swamp forests resembling these are local, occupying parts of the lake plains, marked depressions in the youngest glacial plain, or commonly, small stratum plains on impervious rock. The last are seen on the flats of Devonian shale in Kentucky and Indiana (Muscatatuck Flats), and on level parts of the Allegheny and Cumberland plateaus at the headwaters of streams. Such areas are relatively small in extent, and while they contain some of the species, and have much of the aspect of the swamp forests of the till plains, they nowhere display the complexity of communities or the successional development marking the vegetation of the till plain of southwestern Ohio.

The area under consideration covers approximately 1,500 square miles to the east of the Little Miami River; it is flat or nearly flat upland lying at an elevation of about 900 or 1,000 feet. Throughout its extent, bedrock is buried under a mantle of glacial drift of Illinoian age which varies in thickness from 10 to 50 feet (Fuller and Clapp, 1912). The valleys of the larger streams trench this plain to a depth of 100 to 300 feet; smaller streams except in the immediate vicinity of large ones, flow in shallow valleys few of which cut deeply enough to enter the bedrock. Although this area is far older than the glacial plains to the north which are of Wisconsin age, it, nevertheless, is still topographically young and many places remain as yet undissected by even the smallest streams. Initial inequalities in the drift deposit are indicated by the very shallow depressions only a few feet in depth which are still discernible in many places. These topographic features make for poor run-off and a water-logged soil.

II. HABITAT FACTORS

The habitat is essentially an undissected plain with fine-grained soils, water-logged, and hence poorly aerated. Man's modification of the area by ditching and clearing has made changes which are far-reaching and as a result the habitat of today is not the extreme habitat in which the vegetation developed. Soil water especially, and hence soil aeration and humus decomposition have been affected. Because this is a glacial topography for the most part unmodified by erosion, vegetational development apart from that brought about by climatic changes has in the main been directed by biotic factors.

However, the major vegetational features are due to topography and soil conditions. Bare areas do not exist; pioneer communities have long since been crowded out by later vegetation, and all habitats have been affected by the reaction of vegetation. Certain soil factors, whether antecedent to or resultant from present communities, are significant and are in need of further study.

Temperature and Precipitation

Temperature and precipitation data secured from U. S. Weather Bureau records of one station (near Batavia) on the till plain, and from stations adjacent to the till plain to east, west and north, show essential climatic uniformity throughout this and adjacent areas. Temperature ranges from a January mean of 30°F. to a July mean of 75°F., approximately, with a maximum annual temperature range of about 120°F. The frostless season is nearly 6½ months. Rainfall for the region is approximately 40 inches, fairly evenly distributed throughout the year. Due to the patchy precipitation resulting from summer thunderstorms and the tendency of such storms to follow definite courses, certain areas are less often visited by heavy rains and have the reputation of being "dry islands." These differences do not appear in the few available records. They may have some bearing on the distribution of the characteristic shrub species and be responsible in part for the absence of these shrubs from some large areas. In drought years, the effect is more disastrous in these places. In those areas of the flats in which beech and white oak suffered most from the 1930 drought the characteristic shrubs are most poorly represented, indicating that these areas have in the past suffered in the same manner.

Evaporation

Evaporation, usually considered to be of major importance in ecological work, is here considered to be of little value in explaining differences in adjacent communities. Uniformity of topography and hence initial similarity of evaporation throughout the area—except as affected by differences of rainfall—preclude the possibility of this having been an initial cause. Any differences which may exist now are the result of, not the cause of, differences of forest cover.

Light

Differences in light are due to the amount and kind of vegetation covering, not to any initial conditions. They become extremely important in the course of these biotic successions, perhaps determinative in the ecesis of certain species during successional development. Light as a factor in the germination of seed of sun plants may be important (Hutchings, 1932). Light, however, could scarcely have been a factor in bringing about differences in initial forest stages.

Soils

The soils of the Illinoian till plain are all fine-grained and classified as silt loams. Weathering has proceeded so deeply that few pebbles remain. While all have developed from originally calcareous drift, the soluble carbonates have been leached so deeply that the soils are acid. The earlier soil surveys (Coffey and Rice, 1915; Goodman, Allen and Phillips, 1917) recognized three types of upland soils in this area: the Cincinnati silt loam, the Rossmoyne silt loam, and the Clermont silt loam. Later surveys (Taylor et al, 1928; Conrey, mss. map) have distinguished additional types or subtypes.

The Cincinnati silt loam has attained approximately a mature state of development. It occurs on all of the hillier sections of the glacial plains, usually on the slopes bordering stream valleys. The Rossmoyne silt loam is intermediate in position between the Cincinnati silt loam and the Clermont silt loam. It occupies the very low and scarcely noticeable ridges which traverse some of the flattest areas and occurs as a narrow belt around the borders of the flats.

The Clermont silt loam is most important and gives to the area much of its distinctive character. It is ashy white when dry—hence the name "white clay" which is commonly applied. The subsoil is strongly mottled with brown iron stain. This is the soil which prevails throughout the flattest parts of the Illinoian till plain; throughout most of the area which may properly be designated as "plain." Locally, and usually in the indefinable depressions about the heads of streams, a darker soil has developed—the Blanchester silt loam. The Clermont and Blanchester silt loams have developed under conditions of poor drainage; the Cincinnati silt loam under good drainage; the Rossmoyne, intermediate, and demonstrates the soil changes which have taken place where the marginal part of the Clermont silt loam has been affected by developing drainage lines.

On cleared land, areas of the several soil types are readily distinguished by color. In forest land, the surface layer is slightly darkened by humus in all types, but differences are evident at depths of 4 or 5 inches.

The accompanying map (Fig. 2) shows the approximate extent and location of the Clermont (including Blanchester) silt loam; or, the area of the undissected till plain.

The combination of fine-grained soils with slight or no granulation, exceedingly compact a few inches beneath the surface, and level land undissected by streams results in very poor surface drainage. Water stands in fields and even in forests after heavy rains, and in seasons of normal rainfall, throughout much of the winter and spring months. This introduces a decided handicap to land utilization. Attempts to overcome these conditions and drain the land, thus making it more fit agriculturally, have been made and have resulted in profound changes in the environment. Fields are ditched or tile-

drained or both; ditches 1 to 3 feet deep extend alongside of every road; and "township ditches" collect the water from the field ditches and carry it sometimes several miles to streams. Such township ditches may be 3 to 5 feet in depth, for some flow must be possible during heavy rains if they are to carry off surface water. The meandering, swampy and shallow creek valleys have in many places been straightened and deepened to serve as ditches. In fact it is now difficult to find any which do not flow in straight lines and turn at

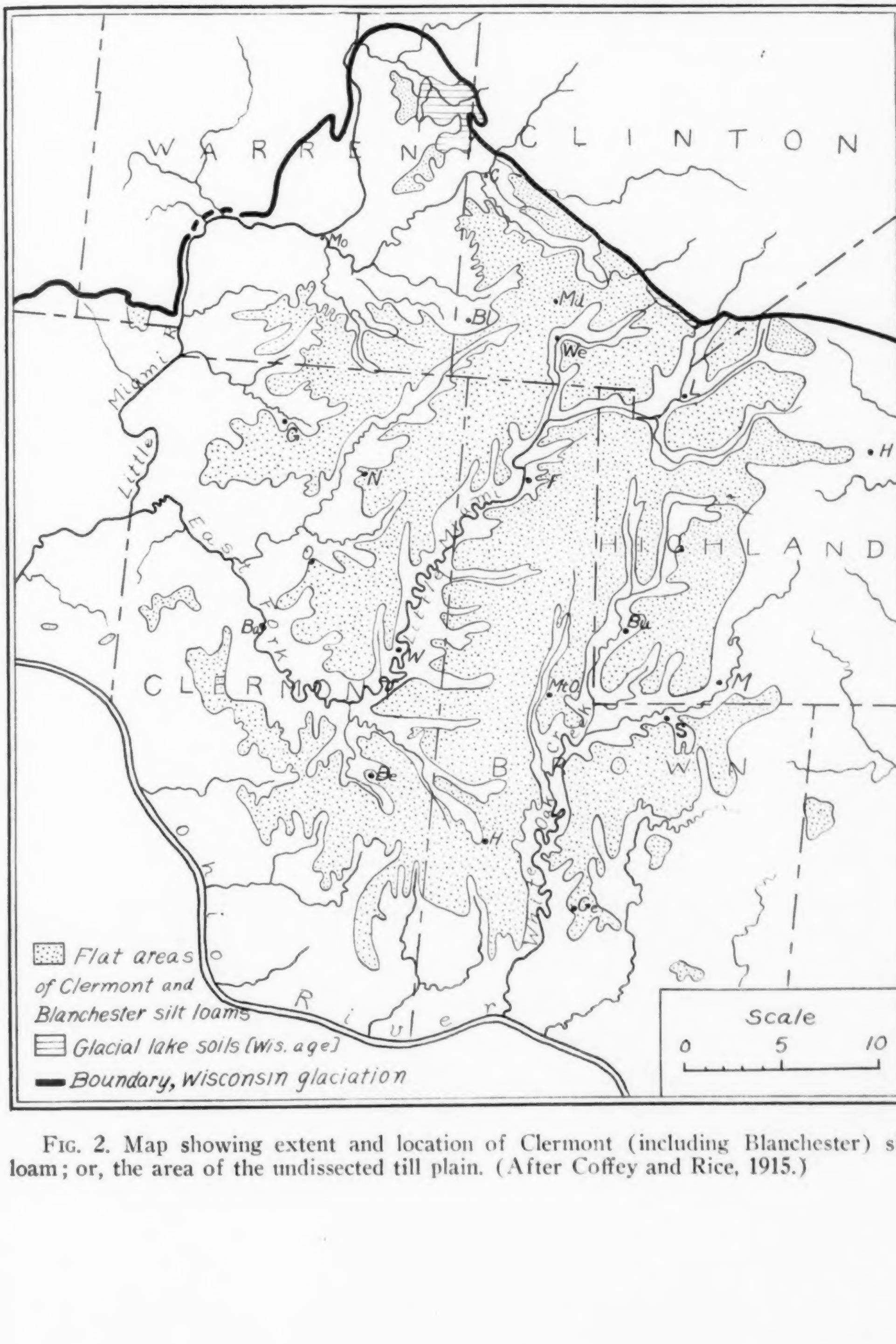

FIG. 2. Map showing extent and location of Clermont (including Blanchester) silt loam; or, the area of the undissected till plain. (After Coffey and Rice, 1915.)

right angles. As these wet flats are within the Revolutionary Land Grant area of Ohio, settlements were made here over 125 years ago and the first clearings made at that time. Most of the changes due to ditching are, however, relatively recent and followed the introduction of tile-drainage and the maintenance of the township ditches. Fields which now grow corn successfully used to stand under water all winter and even all summer in wet years. Farmers tell of places—now fairly good corn fields—where it was necessary for miles to walk logs and jump from root to root in the forest swamp to keep out of the water, even in August. Conditions of this sort no longer exist; the environment under which the existing forest types developed is not represented in the area today. The environmental conditions which now exist —atmospheric humidity, the conditions of soil, soil water, even to some extent soil composition—are not the conditions under which the vegetation of the till plains developed. The environment, unmodified by man, is gone, and the return of forests similar to the original is no longer possible. Neither is the secondary vegetation now coming in like that which started as little as 25 years ago. It is justifiable to assume that previous to disturbance the water table was higher and that ponds were more extensive and more permanent than now.

Soil Water

Measurements of the amount of soil water, unless carried on through enough years to cover entire cycles of weather including periods of extreme drought and of maximum rainfall mean little in an area where extremes of habitat are absent. Also, soil water if measured now, would not indicate the conditions under which any except the youngest secondary communities developed.

Soil Aeration

Aeration is dependent on soil porosity and the level of ground water, which fluctuates with climatic cycles. In average years the water table is at or near the surface in broad flats and above the surface in depressions from about November to May or June. In dry years it is at or close to the surface in depressions; in drought years, many depressions are dry.

Soil Temperature

Due to the high water content, especially in spring, soil temperature is lower than in hillier areas. This results in a retardation of growth in spring which is particularly evident in time of leafing of trees and blooming of shrubs. This difference on the wet flats and on adjacent hilly land may amount to one or two weeks in the same species.

Nitrogen Content and Humus Content

The Clermont silt loam and the Blanchester silt loam, which differ in organic content—the Clermont silt loam "is particularly deficient in organic

matter" (Taylor et al. 1928)—support partly unlike communities. Chapman (1933), experimenting with the effects of nitrogen on the growth of seedlings of tulip tree, selected Clermont silt loam as a medium for growth because of its small content of organic matter. This work indicates that the scarcity on the till plain of tulip, which is not a nitrate accumulating species, may be accounted for by the absence of nitrogen from the soil. The absence of other common mesophytic forest trees from areas of Clermont silt loam may be due in part at least to this factor.

Hydrogen Ion

Hydrogen ion is here a factor of importance only in so far as it exerts a selective influence on certain acid soil species, and in its probable relation to soil organisms and consequent decomposition processes. All of the soils of the till plains are acid, ranging from pH 6.5 to pH 3.5.[1] The range of pH values in the several successional stages and beech subclimax forest is shown in Table 1. From this it will be seen that the soils of initial forest stages are

TABLE 1. Range of pH values of soils at one and five inch depths in the several successional stages and beech subclimax.

pH values	Initial		Intermediate		Late		Climax	
	1 in.	5 in.	1 in.	5 in.	1 in.	5 in.	1 in.	5 in.
3.5 — 3.9	2	..	2	1	2	..	..	..
4.0 — 4.4	10	13	4	7	3	3	1	1
4.5 — 4.9	23	27	5	14	5	9	3	5
5.0 — 5.4	10	1	13	5	2	2	2	3
5.5 — 5.9	..	1	5	1	1	..	6	1
6.0 — 6.4	..	..	1	..	2	1	3	..
Number of samples tested	45	42	30	28	15	15	15	10

somewhat more acid than those of intermediate and late stages, and the range of reactions less than in later stages. There is a slight widening of the range of reactions in later stages, together with a tendency to less acid soils—conditions agreeing with the observations of Geisler (1926).

The yellow Rossmoyne silt loam soils mostly range between pH 5.0 and pH 6.0. The white Clermont silt loam and the darker Blanchester silt loams are generally more acid, pH 4.0 to 5.0. Soils of secondary meadows on the Rossmoyne silt loam have pH values between 5.0 and 5.5; those on Clermont silt loam and Blanchester silt loam, though floristically very distinct, are similar in soil acidity, with pH values between 4 and 5, mostly around 4.5.

The most acid soils are those under Sphagnum and Polytrichum hummocks, and in clumps of Vaccinium. Soils from Sphagnum mounds range

[1] pH values were determined electrically for 312 soil samples, using quinhydrone electrodes. For these determinations, the writer is indebted to Miss Emily R. Hess.

from pH 3.6 to 4.2; from Polytrichum mounds, pH 3.5 to 4.2; from among Vaccinium bushes, pH 3.8 to 4.8.

A few of the plants sometimes found in forest communities, as *Mitchella repens*,[2] *Chimaphila maculata*, *Vaccinium vacillans* and *V. stamineum*, are generally recognized as acid soil species, rather than swamp species. A few commonly require acid soil and abundant moisture; among these are *Sphagnum subsecundum* Nees, which is locally abundant, *Aspidium noveboracense*, *Spiraea tomentosa* and *S. alba*, *Pyrus melanocarpa*, *Viola lanceolata*.

There is little relation between pH and topography, except where dissection is sufficient to introduce drained slopes (see transect, Fig. 34). pH values for soils in areas of transects are shown along the profiles accompanying transects (Figs. 28, 30, 32, 34). No significant differences could be observed between pH values of the earlier stages of the PO → WO → B and RM → B successions.

Root Competition

Observations on the root systems of a number of plants indicate that adaptability of root system and root competition in the upper soil layers are important factors in determining the ability of plants to occupy these areas. The conditions of soil water and soil aeration are unfavorable to deep root penetration.

The adaptability of beech, permitting it to develop a very shallow root system in the wettest and most poorly aerated soils, may account in part for the early entrance of this mesophyte in succession. It also results, in times of severe drought, in the dying out of this species in depressions, thus opening up small areas for re-invasion by trees.

The development of shallow root systems by beech, white elm, red maple and occasionally sweet gum increases root competition in all areas where these trees are present, and may be a factor in accounting for the paucity of ground vegetation in those communities in which these trees are important. Under beech trees in the wettest places—where the mat of fine fibrous roots fills the upper 3 to 5 inches of soil—only such superficial plants as *Mitchella repens* can grow. On the other hand, the greater abundance of shrubs and herbs in many pin oak and white oak areas (neither of which trees develop shallow root systems) may be due in part to the lesser competition in these communities. Peculiarities of the root systems of some of the plants of the till plain have been considered in a separate paper (Braun, 1936).

Topographic Factors

Topographically, the habitat is a plain, almost level, which here and there contains depressions a few inches or a few feet in depth, or ridges of like proportions. These minor inequalities in the land surface result in differences

[2] Nomenclature in this paper according to Gray's New Manual of Botany, 7th Ed., 1908, except as noted.

in the soil water factor which are reflected in the distribution and grouping of tree species in the forest. The sequence of communities in and around depressions and the sequence from ravines to flats are definitely related to topography. This is demonstrated by a series of transects, Figures 28, 30, 32, 34.

III. PRIMARY VEGETATION

The original forest of the undissected till plain was a mixed forest composed of about 15 tree species segregated into more or less distinct communities in different stages of successional development. In the forest as a whole, beech, white oak, pin oak, red maple, white elm, shellbark hickory and sweet gum are, in the order named, the most important species. Of this original forest, only isolated remnants remain, few of which are as large as 100 acres. Because of this, the relation of communities to habitat, the inter-relations of communities and successional development are often obscured.

All of the forest communities, of which there are about 25 distinguishable, belong to hydrarch successions in which three developmental stages are recognizable: (1) Initial forest stages; (2) Intermediate stages; and (3) Late stages. The initial forest stages are not pioneer—the pioneer vegetation of these wet uplands entered many thousand years ago with the first invasion of plants into the new glacial deposits; the late stages may be thought of as resulting in a physiographic climax, to persist as long as the till plain remains undissected and undrained. Drainage permits the entrance of other mesophytic species and in time results—if stream cutting does not go too far—in the development of the mixed mesophytic forest, the climatic climax of this geographic area.

Initial forest stages include several segregates of what may be termed the pin oak-red maple-elm-sweet gum associes. They occupy depressions, many of which are not deep enough for the surface of the ground to appear damp in summer, though it may at times be covered with shallow water. Depressions are usually small, a few hundred feet across, and seldom do all of the species occur in any one depression.

Intermediate stages are marked by the appearance and increasing importance of species which later become dominant or codominant, namely, shellbark hickory, white oak, and beech; and by the disappearance, first of pin oak, later of white elm, sweet gum, and red maple.

The white oak-beech associes and certain phases of the beech forest are late stages; the beech association may be considered the climax of the undissected areas, *i.e.*, a physiographic climax. The rims of depressions, the low ridges, and the margins of the plain indented by the shallowest ravines support beech or white oak or a mixture of these two species, together with an admixture of other more or less mesophytic species. All intermediate locations,

and some of the depressions and some of the ridges, if broad, support the intermediate forest stages.

Dissection changes the water relations, and initiates new conditions which cause the disappearance of all hydro-mesophytic species and permit the entrance of mesophytic species. The forest of areas where dissection is beginning approaches the regional climax type—the mixed mesophytic forest of southwestern Ohio and adjacent areas.

Vegetational development on the till plain is shown by the diagram (Fig. 3) of primary successions. All combinations of the constituent species of each stage are possible and lead to considerable complexity and overlapping of communities. The accompanying chart (Fig. 4) shows tree occurrence and importance in developmental stages of the till plain forest and in the physiographic and regional climaxes, based upon counts in primary areas.

In Table 2 are listed all of the trees, in the order of the presence percentage[3] of the species. Presence percentage (Pr %) is determined from occurrence in 50 forest areas of the till plain for which composition lists were made. The low presence percentage of sweet gum—considered one of the important trees of the swamp forest—is due to its almost complete limitation, geographically, to the southern half of the area. The percentage of each species in the forest of the till plain as a whole, based upon a count of 3,707 trees, is also given. Additional columns in the table give the forest canopy composition of nineteen representative areas of primary forest in the flats,

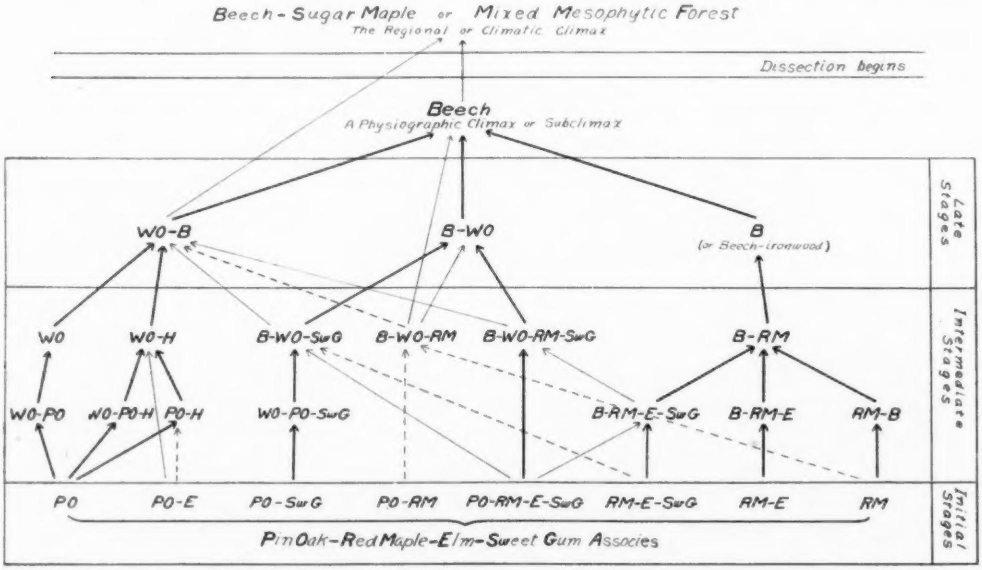

FIG. 3. Diagram of primary successions on the till plain.

[3] By presence is meant the more or less persistent occurrence of a species in all the stands of a certain community." Braun-Blanquet (1932). As defined by Cain (1932) "Presence concerns the degree of regularity with which species reoccur in different examples of an association." This may be expressed in percentage (as in Table 2) or, less exactly, in the 1 to 5 scale suggested by both Braun-Blanquet and Cain.

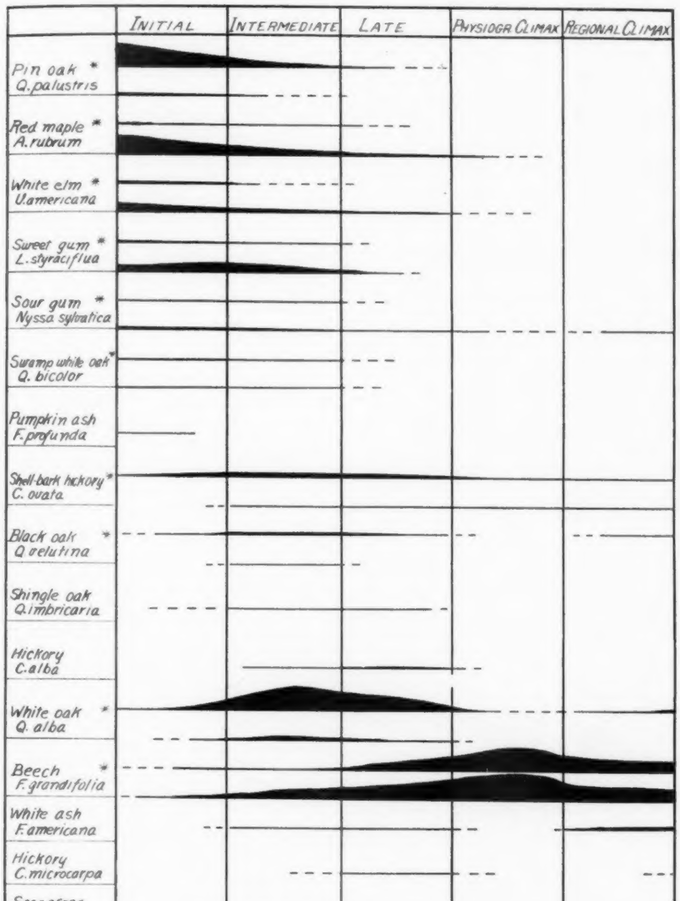

FIG. 4. Chart of tree occurrence and importance in developmental stages of the till plain forest and in the physiographic and regional climaxes, based upon counts in primary areas.

TABLE 2. Percentage Composition of Trees of Forest Canopy in Representative Areas of Developmental and Climax Stages of Succession on the Till Plain and of the Regional Climax.

	AREA AS A WHOLE		INITIAL STAGES						INTERMEDIATE STAGES												LATE STAGES					PHYSIOGRAPHIC CLIMAX OR SUBCLIMAX			REGIONAL OR CLIMATIC CLIMAX		
	Pr. %		PO			PO-RM-E-SwG & RM-E-SwG			WO-PO-SwG, WO-PO & WO				B-RM-E-SwG & B-RM-E				B-WO-RM & B-WO-SwG				WO-B					B			Mixed Mesophytic		
Number of trees		3707	208	172	400	77	82	190	32	63	120	295	249	70	60	379	148	120	187	674	349	210	191	357	1309	213	171	384	75	126	405
Forest area, number	...	...	1	2	...	3	4	...	5	6	7	...	8	9	10	...	11	12	13	...	14	15	16	17	...	18	19	...	20	21	...
Fagus grandifolia, beech	86	36.2	1.4	1.6	1.2	14.6*	14.6*	14.2	...	...	...	2.0	37.7	51.4	76.6	46.7	24.3	49.2	50.8	43.6	21.5	31.4	37.2	39.5	34.6	80.3	88.3	83.8	62.6	47.0	42.4
Quercus alba, white oak	80	23.0	8.2	19.2	12.5	1.3	2.4	1.6	31.2	65.1	78.9	68.8	.4	10.0	...	4.5	29.0	26.6	23.0	20.5	39.5	30.0	31.9	33.3	34.4	1.4	...	.8	...	.8	2.0
Carya ovata, shell-bark hickory	80	4.9	8.2	4.6	6.2	...	...	...	9.0	9.5	6.6	7.4	2.4	...	1.6	1.8	5.4	1.6	2.6	4.1	13.7	9.0	1.6	4.5	6.8	4.2	2.3	3.4	...	.8	.7
Quercus palustris, pin oak	74	11.1	71.2	63.4	67.5	37.7	...	16.8	21.9	12.7	6.6	8.4	4.8	...	...	3.2	6.1	7.5	1.0	3.5	6.3	6.2	4.7	2.5	4.2	...	...	...	...	...	...
Acer rubrum, red maple	72	7.3	.5	...	.7	9.1	46.3	27.9	3.0	...	.7	.7	14.8	14.3	8.3	13.7	18.2	3.3	7.0	8.4	1.2	7.1	8.9	12.0	6.7	4.7	1.2	3.1	...	...	...
Nyssa sylvatica, sour gum	66	2.8	.5	5.8	2.7	9.1	4.9	6.3	3.1	...	...	1.0	8.0	...	...	5.2	...	...	2.1	4.6	1.2	3.1	1.0	2.0	1.8	.5	1.2	.8	1.3	.8	1.2
Ulmus americana, white elm	58	5.0	5.3	1.6	4.0	14.3	17.1	20.0	...	...	...	...	11.2	4.3	11.6	10.0	9.5	...	1.6	4.4	2.0	3.1	7.8	3.1	3.0	7.5	7.0	7.3	...	...	.5
Quercus bicolor, swamp white oak	46	1.1	3.3	3.2	2.7	5.2	...	3.1	12.5	6.4	...	3.0	1.2	1.4	...	1.1	...	...	.5	.1	1.6	.5	.5	.8	.8	...	...	...	...	...	...
Liquidambar styraciflua, sweet gum	40	3.5	...	...	.5	9.1	13.4	9.5	15.6	...	...	2.4	12.4	17.1	...	11.3	...	11.6	10.2	8.6	...	.5	...	...	.4	...	...	...	...	...	...
Quercus velutina, black oak	40	1.8	1.4	3.2	1.7	...	...	...	3.0	3.2	6.6	4.4	...	...	...	...	4.7	...	.5	1.2	8.9	2.0	1.6	.5	3.1	...	...	...	...	...	.3
Quercus imbricaria, shingle oak	28	.2	...	...	...	...	...	...	...	3.2	...	.7	...	...	...	...	2.0	...	...	.4	...	1.0	.5	...	.3	...	...	...	...	...	...
Carya alba, white-heart hickory	26	.7	...	...	...	...	...	...	...	...	.7	.3	.8	...	...	.8	...	...	...	...	2.5	4.7	.5	...	1.8	...	...	...	...	...	...
Fraxinus americana, white ash	20	.4	...	...	...	...	1.2	.5	...	...	...	...	.4	1.4	...	.3	...	...	...	...	.3	2.0	.5	...	1.0	...	...	...	2.6	6.3	5.0
Acer saccharum, sugar maple	10	.2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	.6	...	...	2.1	.6	...	...	...	8.0	15.0	14.8
Liriodendron tulipifera, tulip tree	8	.1	...	...	...	...	...	...	...	...	...	...	2.0	...	...	1.3	...	...	...	...	...	...	...	...	...	...	...	...	17.3	13.5	12.0
Quercus rubra, red oak	8	.1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	.2	.1–	1.4	...	.8	...	4.0	1.2
Carya microcarpa, small-fruited hickory	6	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	.5	.1	...	...	...	...	.1–	...	...	...	...	...	...
Carya cordiformis, bitternut hickory	6	.1	...	...	...	...	...	...	...	...	...	...	...	...	1.6	.3	.7	...	...	.1	...	...	...	...	.1	...	...	...	1.3	.8	1.2
Fraxinus pennsylvanica, red ash	4	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Fraxinus profunda, pumpkin ash	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Sassafras variifolium, sassafras	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Tilia americana, basswood	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1.3	4.0	9.1
Juglans nigra, walnut	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1.3	5.5	3.2
Ulmus fulva, red elm	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1.3	...	2.0
Prunus serotina, wild black cherry	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1.3	...	1.7
Celtis occidentalis, hackberry	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1.3	.8	.7
Quercus Muhlenbergii, chestnut oak	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	.7
Carya glabra, pignut	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	.5
Aesculus octandra, sweet buckeye	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	.3
Juglans cinerea, butternut	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	.8	.3

*Beech mostly smaller than characteristic trees of initial forest stages but too large to be ignored; indicates approach toward intermediate stage.

and for comparison, of two areas of mixed mesophytic forest—the regional or climatic climax. These are grouped in successional stages, and demonstrate something of the variations in composition and in importance of constituent species possible in the several stages. For each segregate or group of segregates of the associes of the several stages the percentages are listed; these are based on the counts given for the selected areas and a few additional counts. In all cases the number of trees from which the calculations were made is given. The occurrence, in forest communities referred in this table to "initial stages" of trees more characteristic of later stages, is due to humps and land surface inequalities which offer a fairly suitable environment to trees normally occurring later. Similarly, the occurrence in "late stages" of trees of the initial stages is due either to the occurrence of scattered very small depressions in which one or several pioneer trees persist (the group really not a part of the later successional stage by which it is surrounded) or to windfalls which have resulted in lighter places more suitable to pioneer species. These features of distribution are amply demonstrated in transects charted in a number of representative forest areas (see Figures 28, 30, 32, 34).

Shrubs are abundant in the forests of the till plains, and constitute a floristically important element of the vegetation. Thirty-five species including six woody climbers are recorded—several times the number which occur in any one successional series in the edaphically-diversified adjacent Cincinnati region. The most characteristic of the shrub species are: *Ilex verticillata* (4+), *Viburnum pubescens* var. *indianense* Rehder (4+), *Vitis labrusca* (4), *Spiraea tomentosa* (3+), and *Pyrus melanocarpa* (2-3). These are fairly generally distributed in the area (Braun, 1935a); presence is indicated by the numerals in parenthesis (following the 1-5 scale). Certain other rarer species are peculiar to the till plains, *i.e.*, do not occur in the regions to either side; these are *Spiraea alba*, *S. latifolia*,[4] *Rubus hispidus*, and *Viburnum Lentago*. Two species of Vaccinium *(V. stamineum* and *V. vacillans)* occur rarely; both are abundant in the Allegheny Plateau but local west of that section. A number of other shrubs, though not peculiar to the Illinoian plain, are abundant; among these are: *Cephalanthus occidentalis, Salix discolor, Rosa carolina (R. palustris), Rosa setigera, Viburnum prunifolium, Corylus americana, Cornus racemosa*[5] *(C. candidissima), Cornus obliqua*,[5] *Hypericum prolificum, Smilax Bona-nox*. For each of these the index of presence is 3 (except *Rosa carolina*, 4), lower than for most of the more characteristic species, though when present these species often occur in larger patches than do any of the others except *Spiraea tomentosa*.

The community relations of most of these shrubs are obscure, for they are most common at the edges of forests and in clearings or secondary meadows. All, however, occur in initial or intermediate stages of the primary

[4] Specimen referred by E. J. Alexander of the New York Botanical Garden to *Spiraea latifolia*.
[5] Fide E. J. Palmer, Arnold Arboretum.

forest, but do not flower or fruit as freely in the forest as in more open situations. In later successional stages, occasionally also in intermediate stages, a few common mesophytes appear, especially *Benzoin aestivale*, *Sambucus canadensis* and *Asimina triloba*. In any stage of the forest succession, poison ivy *(Rhus Toxicodendron)* may be present and so abundant as to dominate the ground layer. *Viburnum prunifolium* is peculiar in its ecological distribution, occurring occasionally in initial and commonly in intermediate stages in these hydrarch successions, and abundantly as a pioneer in xerarch successions of river and ravine slopes of the same geographic area.

The number of species of herbaceous plants in the primary communities is fewer than in surrounding dissected areas. Nowhere except in the openings is the ground at any time clothed with an herbaceous layer. The forest is remarkably poor in herbaceous plants. Very few of the plants of the mesophytic or xero-mesophytic forests of slopes are here, and few swamp species endure the dense shade. The usual display of vernal flora of deciduous forests is absent, though a few species—*Cardamine bulbosa, Ranunculus hispidus* var. *falsus* Fernald, *Polemonium reptans, Claytonia virginica* and sometimes *Anemone quinquefolia, Arisaema triphyllum*, and *A. Dracontium*—are scattered in the swamp forest. In the later successional stages, a few additional plants of the spring flora enter, especially *Podophyllum peltatum*. A number of more or less distinctive plants, absent or rare in adjacent areas, are found; some of these are mentioned here. *Mitchella repens* is abundant in mossy hummocks about tree roots and on the ground in later forest stages; *Chimaphila maculata, Medeola virginica, Uvularia perfoliata, U. sessilifolia*, and *Tipularia discolor* occur in intermediate or late forest stages. Among the plants of openings in the pin oak forest are *Phlox maculata* var. *odorata* (Sweet) Wherry, *Aureolaria (Dasystoma) flava* var. *macrantha*,[6] *Habenaria peramoena, Lobelia cardinalis, Viola cucullata, Aster umbellatus, Lilium canadense*, and *Gentiana Saponaria*. *Rhexia virginica, Viola lanceolata, Houstonia coerulea, Coreopsis, tripteris*, and some of the plants of the pin oak openings are more or less characteristic of meadow communities. Ferns are represented by *Onoclea sensibilis, Asplenium angustum* (Willd.) Presl. and *Aspidium Thelypteris* (all locally forming large patches); *Osmunda regalis* (in both meadow and forest communities); *Botrychium obliquum* (always scattered but generally present); and *Botrychium dissectum*.

Mosses are abundant and very prominent in early successional stages, becoming less so in intermediate stages, except on beech roots in very wet forests. Most important are species of Polytrichum, Catharinea, Mnium, Dicranum, Leucobryum, Thuidium, Climacium and Sphagnum. Of these, *Climacium Kindbergii* (R. & C.) Grout and *Sphagnum subsecundum* Nees are characteristic of the more open and wettest places.

[6] Determined by F. W. Pennell, Academy of Natural Sciences, Philadelphia.

The forest of the till plain is, then, a mixture of hydro-mesophytic tree species, with which are associated certain shrub and herb species, which because of their community and geographic limitations, are peculiarly characteristic of the area under consideration. More detailed features will be treated with the discussion of the various forest stages and successions.

A. INITIAL FOREST STAGES

1. DEPRESSIONS

Developmentally, the *pin oak-red maple-elm-sweet gum associes* is the youngest forest stage of these glacial plains. It is rarely represented as an associes with four dominants, but more often as segregates[7] in which one to three of the above species dominate, and in which swamp white oak and sour gum may be present as secondary species.

Area 3 (Table 2) gives percentages of one area in which the four important trees of this initial forest associes occur together. This area is a depression from 3 to 4 feet lower than the surrounding area of beech-white oak-sweet gum forest (no. 12 of Table 2). It is a rather dense stand, though in the central (and lowest) part of the depression the trees stand farther apart, and young pin oak, red maple and sweet gum are entering. Except in the lowest part, this depression forest is somewhat past the pioneer forest condition and the admixture of beech marks the transition to the beech-white oak-sweet gum associes of the surrounding plain.

The most prevalent of the initial forest stages is the pin oak consocies, which is so much more important over most of the area than any other that it may be thought of as the most characteristic forest of depressions.

Pin Oak Consocies

The pin oak forest or pin oak opening at its best is an almost pure stand of pin oak in rather open or park-like formation, with a sedge ground layer (Fig. 5). In spring the entire sedge area may be covered with shallow water. The pin oaks usually range in size from 7 to 9 feet in circumference, b.h., occasionally reaching 11 or 11½ feet. Similar areas of younger trees, 4 to 5 feet in circumference, are sometimes seen. Some of these are primary, some secondary; this may usually be determined by position and successional contacts. Swamp white oak, sour gum, white elm, sweet gum, or occasionally white oak, may be present. Swamp white oak in these depressions may be 9 to 10½ feet in circumference. Most often, this forest contains very few small trees. The ground cover is dominantly sedge—*Scirpus atrovirens, Carex typhina, C. squarrosa, C. lupulina, C. Asa-Grayi, C. intumescens, C. crinita,*

[7] Segregation and regrouping of the dominants of complex communities give rise to a variety of communities with different dominants. Segregates of the associes, as in the above instance, are associes-segregates. The term, associes-segregate, includes consocies, facies, and locies. The association-segregate is a climax unit (see Braun, 1935).

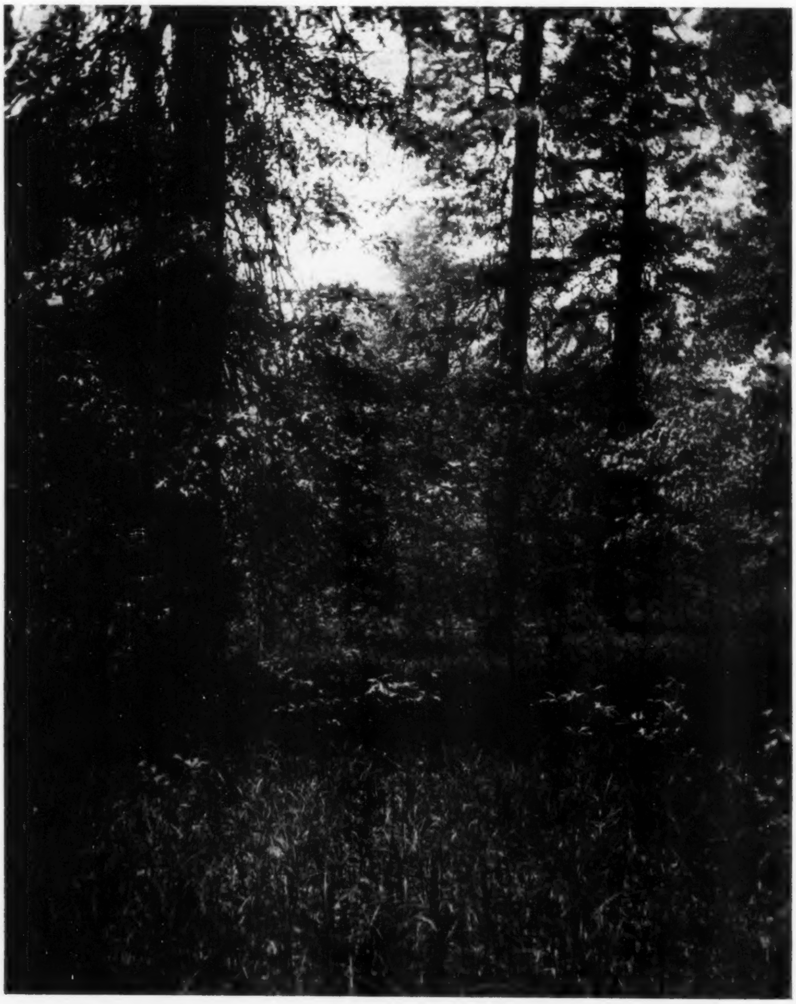

FIG. 5. Pin oak opening with sedge ground cover. Scattered small pin oaks point to future closing in of forest. May.

C. grisea, C. gracillima, C. caroliniana, C. tribuloides, and *C. stipata*.[8] In spring, *Cardamine bulbosa, Polemonium reptans,* and *Ranunculus hispidus* var. *falsus* Fernald are conspicuous. *Phlox maculata* var. *odorata,* blooming in early June, is locally abundant (Fig. 6). *Lobelia cardinalis* is commonly present, and often *Chelone glabra* and *Habenaria peramoena. Aster umbellatus, Eupatorium maculatum, Solidago rugosa,* and *S. canadensis* are of frequent occurrence. *Ilex verticillata* and *Rosa setigera* are usually present.

Successionally older pin oak areas have a scattered stand of small pin oak and shellbark hickory as an understory. Their entrance does not at first change the aspect of the open forest; later, with decrease in light, the sedge ground cover becomes thinner and patchy. In places a very dense layer of small pin oak is seen, completely filling the space between the widely-spaced

[8] Species of Carex determined by K. K. Mackenzie.

older trees, and eliminating all intolerant herb and shrub species of the openings (Fig. 7). Such mass growth of young trees seems to be correlated with the sudden lowering of the water table by ditching: the sedge pond is changed to a wet flat; soil aeration is improved; the light conditions are still favorable for intolerant species, and pin oak enters in great density. Such areas are usually devoid of undergrowth though poison ivy may be present. The ground is covered by a mat of soggy oak leaves; standing water is clear but brown.

The gradual lessening of light with increasing numbers of trees more and more limits the area suitable to meadow herbs and shrubs. Thus these become limited to very small areas. The rarer species, seen only occasionally though sometimes abundant or dominating in the opening in which found, may have thus been circumscribed. Two such species are *Baptisia leucantha* and *Aureolaria flava* var. *macrantha,* each seen in but one opening.

It would seem probable that the shrubs and herbs previously mentioned as peculiar to the flats but most abundant along forest borders and in secondary meadows originally belonged to openings and pin oak openings, but have now been obliterated there with the closing in of the forest, a process locally hastened by the artificial drainage in the area. In one opening,[9] twelve of the shrubby plants previously listed occur; these include the five most characteristic shrubs *(Ilex verticillata, Viburnum pubescens* var. *indianense, Vitis labrusca, Spiraea tomentosa, Pyrus melanocarpa)* and one *(Spiraea latifolia)* found only here. Eleven of the more characteristic herbaceous plants in addition to sedges and grasses are here also. The trees of the opening are

FIG. 6. *Phlox maculata* var. *odorata* in pin oak opening. June.

[9] Northwest of Blanchester, in Warren County.

relatively small—averaging about 4 feet in circumference—but the aspect is characteristic of the typical pin oak opening. The location of this opening, at the end of a rather elongate but irregular second growth stand of pin oak might cast some doubt upon its primary nature. However, the trees here are larger, older, and more unevenly aged than in the adjoining secondary forest, but not old enough to have been cut for timber at the time the adjacent forest was cut. This opening and several others undoubtedly primary, in which one to several of the more characteristic of the intolerant shrub and herb species occur, give good evidence that these species were plants of the sedgy openings and open pin oak areas. They have been almost eliminated within the forest by the gradual closing in of the trees, but have reproduced abundantly when and where the forest was cut but the land not tilled. In the utilization of forest areas for grazing, the openings suffered much. Furthermore, here were depressions where shallow but permanent ponds could easily be dug for water for the cattle. Thus often, the youngest places, successionally, have been most completely destroyed.

The soil on which these pin oak communities are found is the Clermont

FIG. 7. A dense stand of small pin oak with some swamp white oak has changed this depression from an open pin oak-sedge community to a deep shade area almost without undergrowth. Though young, this pin oak stand is primary. One of the large trees of the depression, a swamp white oak, is seen to the left.

silt loam—the "white clay." The topographic relations may be seen from the transect, Fig. 30, which passes through two pin oak-sedge areas. The composition of the typical pin oak consocies is shown by area 1 (Table 2); it is this area which the transect, Fig. 30, crosses. Area 2 (Table 2) is successionally slightly older and hence contains a higher percentage of white oak.

Variations of the Pin Oak Consocies

Departures from the typical pin oak consocies occur, due to combinations of pin oak and other of the important trees of the associes or to local dominance of secondary species, as swamp white oak. Pin oak-sweet gum, pin oak-elm, and pin oak-red maple occur. Areas supporting these combinations are usually small in extent, scarcely noticeable depressions containing perhaps a dozen trees. They may, perhaps, be considered distinct segregates of the pin oak-red maple-elm-sweet gum associes, but they are relatively unimportant in the area as a whole. They are usually less open and less sedgy than the typical pin oak areas.

Red Maple, Red Maple-Elm, and Red Maple-Elm-Sweet Gum Associes-Segregates

Red maple is second in importance among the trees of depressions (Fig. 8). It, however, is not often associated in any considerable number with pin oak, but occurs separately, dominating the depression forest community, or with elm or elm and sweet gum. These forest communities may be open, without

FIG. 8. Large red maple in depression about two feet lower than surrounding beech woods. November.

lower tree layers and with an herbaceous layer of sedges and *Cinna arundinacea;* or dense, with scattered small trees in the understory (usually of the same species and in addition beech) and a very poor herbaceous layer. Locally, Carpinus forms the understory, growing in very dense masses; these areas are almost devoid of ground cover (Fig. 9).

Red maple in these areas is one of the large forest trees, usually 9 to 10 feet in circumference, b.h. Its root system is shallow, many of the large roots being on the surface for about ten feet from the trunk. White elm has greatly enlarged bases, almost in the form of plank buttresses; many large roots lie at the surface of the ground or arch upward several inches (Braun, 1936). The trunks above the flaring base often measure 11 feet, sometimes 12 feet in circumference. Sweet gum is usually less massive but taller, the trunks scarcely tapering, and from 6 to 10 feet in circumference, b.h. (Fig. 10). Its roots seldom spread upon the surface of the ground. All roots which are elevated a few inches above the ground level, and hence with their upper surfaces seldom submerged, are moss-covered and moss cushions extend out around them forming hummocks.

The more open red maple or red maple-elm-sweet gum areas resemble somewhat the pin oak openings, though never is the park aspect so pronounced (Fig. 11). The wood reed-grass, *Cinna arundinacea,* is often the dominant

FIG. 9. Ironwood *(Carpinus caroliniana)* with small red maple and sweet gum in depression. Large red maples occupy other parts of this depression. The sparse ground layer includes scattered plants of *Ranunculus hispidus* var. *falsus.*

FIG. 10. Sweet gum in depression. May.

FIG. 11. Lowest and most open part of a depression with red maple, elm, and sweet gum widely spaced; luxuriant herbaceous ground cover in and around the pools which may be seen in center and right foreground. May.

ground cover, or is codominant with sedges (Fig. 12). In the sedge-grass mat, or locally supplanting it, *Ranunculus hispidus* var. *falsus, Phlox maculata* var. *odorata, Chelone glabra, Onoclea sensibilis, Polygonum arifolium, P. sagittatum, Viola cucullata, Lobelia cardinalis,* and other herbaceous plants and ferns are present (Fig. 13). Shrubs are few; *Ilex verticillata* and *Viburnum pubescens* var. *indianense* of the "characteristic shrubs" have been found, but none of the others. In denser stands, the sedge-grass layer is absent and very few herbaceous plants occur. Mosses are conspicuous.

In successionally older red maple depressions, beech is important in the understory foreshadowing its later co-dominance with red maple in the canopy of an intermediate forest stage. Where beech is present in depressions, its roots are very prominent on the surface of the ground, and arch upward sometimes 6 inches. The entire trunk may be elevated, the main roots then appearing as prop roots. Moss mats composed most commonly of Climacium, Thuidium, Polytrichum, Dicranum, Leucobryum and Sphagnum are especially prominent about the beech roots. *Mitchella repens* is abundant in such locations. If the trees are not too closely placed, *Impatiens biflora, Polygonum arifolium, P. sagittatum, Boehmeria cylindrica,* and other coarse herbaceous plants may occupy the depression.

The soil of the red maple depressions—or other communities in which

FIG. 12. Swamp forest in which the wood reed-grass, *Cinna arundinacea*, forms the ground cover. The trees are sweet gum, sour gum, and beech. Rice cut-grass, *Leersia oryzoides*, in and around the pool.

red maple is one dominant—is darker than in the pin oak depressions. That of many of these depressions is classified as Blanchester silt loam.

Area 4 of Table 2 gives the composition of the forest of one of the larger areas of the red maple-elm-sweet gum associes-segregate. The chart, Fig. 14A, is a representative plot in this area. The transect, Fig. 28 (in area 8 of Table 2), passes from a red maple-elm-sweet gum depression up to white oak-beech. The transect, Fig. 32, ends in a red maple depression in advanced stage of development—one in which beech is important in the understory.

2. RAVINE HEADS AND SHALLOW SWAMPY RAVINES

Certain of the indefinable depressions of the till plains, if followed radially in some direction, are seen to have outlets leading to shallow swampy ravines. Such ravine heads are just as imperceptible, topographically, as are the depressions, and bear much the same moisture relations to the surrounding flats. They are not to be likened to the beginnings of ravines working headward; their existence is due to inequalities in the drift surface, not to active erosion. The soil of these ravine heads is usually dark and referable to the Blanchester silt loam. Pin oak is not usually important; red maple or red maple and elm are almost always dominant. Carpinus as an understory to

FIG. 13. Buttercups, *Ranunculus hispidus* var. *falsus*, with scattered clumps of sensitive fern, *Onoclea sensibilis*, form a continuous ground cover in this swamp forest of red maple, elm, and sweet gum.

red maple is not unusual. In two areas—one in Warren County and one in Brown County—pumpkin ash *(Fraxinus profunda)* occurs.

Shallow ravines with definite valley flats and meandering and sometimes anastomosing sluggish streams traverse some of the upland areas. Such ravines have all the characteristics of old valleys and differ greatly from the V-shaped ravines cutting into the plain around its margin. They are, in fact, remnants of an older erosion cycle whose streams have not yet been rejuvenated. The valley flats of these streams support swamp forest of the same type as the glacial plain. White elm is always the most important tree, and with it may be a few other species as pin oak, shingle óak, and green ash (Fig. 33A). The forest of the slope is white oak-beech, an advanced successional stage. The transect, Fig. 32, crosses such a ravine in area 16 (Table 2).

B. Intermediate Forest Stages

The trees of the initial forest stages are, with the exception of sweet gum, intolerant; while they will reproduce for a time in open stands, they do not become established in closed stands even though no appreciable filling of depressions has taken place and hence no change in water relations. More tolerant species will enter, and some one of the intermediate stages develop. Hence forest communities of these intermediate stages may occupy depressions as deep and as wet as those occupied by initial forest stages.

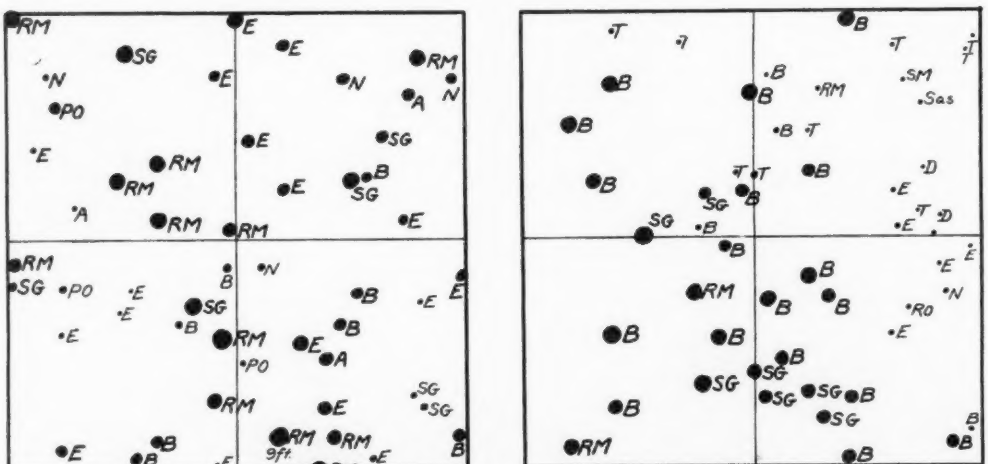

Fig. 14 (A). Representative plot in red maple-elm-sweet gum associes segregate. (B). Representative plot in beech-red maple-elm-sweet gum community. This plot is 150 feet from A and lies at a level 2.5 ft. above that plot. (For key to symbols see p. 129.)

A lowering of the water table, due either to gradual elimination of the depression by filling—a process which is so slow as to be almost negligible—or to stream dissection, permits the entrance of less hydrophytic trees and results in the development of intermediate forest stages. Decrease in light is then an auxiliary factor. Successions resulting either from lowered water table or decreased light or a combination of causes are similar, though in many instances beech increases in importance earlier in succession where decreasing light appears to be the most important causal factor.

The composition of the initial stage determines in part the composition of succeeding communities. White oak-pin oak or white oak forests (with or without an admixture of hickory)—forests of the type illustrated by areas 6 and 7 (Table 2)—succeed the pin oak consocies. Beech-red maple, beech-red maple-elm, or beech-red maple-elm-sweet gum—forests of the type illustrated by areas 8, 9, and 10 (Table 2)—succeed the initial forest stages in which red maple is important. A third developmental group is illustrated by areas 11, 12, and 13 (Table 2). The successional relationships are discussed later.

White oak always appears in intermediate stages in succession when pin oak was present in initial stages (see transect, Fig. 30; beech always enters early in succession when red maple was prominent in initial stages (see transect, Fig. 32). To what extent differences in successional trend are due to initial differences in the environment, to chance distribution and hence prior occupancy, or to the reactions of the initial species on the environment have not been determined. Red maple and elm usually occupy areas of Blanchester silt loam—a darker soil with higher organic content than the Clermont silt loam. Differences in the amount of nitrogen yielded in decomposition of different kinds of leaf litter have been demonstrated by Melin (1931). Lundegårdh (1931) also mentions the specific action of different kinds of decaying vegetation. Such differences are continuing and cumulative. Reactions of the occupying vegetation may be determinative as to the nature of later vegetation.

White Oak-Pin Oak Forest Community

The invasion of the pin oak consocies by white oak or hickory, or by white oak and hickory leads to the establishment of transition communities in which these trees are more or less codominant with pin oak. Most important of these transition phases is the white oak-pin oak forest in which hickory may be an important species; locally, pin oak and hickory dominate, the white oak entering later. Sweet gum may be present; if present in initial forest stages it reproduces and persists in the transition phase, forming a white oak-pin oak-sweet gum forest (Fig. 15). Swamp white oak continues as a secondary species of some importance; black oak enters with white oak. The composition of forests of this type is shown by areas 5 and 6 (Table 2).

The canopy of the white oak-pin oak forest is more continuous than is that of the typical pin oak opening. Usually, saplings are more numerous in the understory and the forest as a whole is dense. Sedges drop out, as do all of the sun swamp plants of the pin oak areas. Of the shrubs, only *Ilex verticillata* and *Viburnum pubescens* var. *indianense* remain. Herbaceous plants are few. This forest is distinctly a transitional step in the establishment of the white oak or white oak-hickory forest.

Fig. 15. White oak-pin oak-sweet gum forest in which smaller beech trees are present. This is in a low part of area 13 (Table 2).

White Oak or White Oak-Hickory Associes

White oak may dominate over large areas, forming a long-lived community occupying a definite position in succession (Figs. 16, 17). Shellbark hickory may or may not be important. Locally, small groves of white oak occur in areas of mixed forest (see parts of transects, Figs. 30, 32); these, too, appear to occupy a definite successional position, rather than to represent local segregates or consocies of a mixed forest community.

The white oak consocies varies from a dense forest with a young tree understory and poor herbaceous ground layer (the usual condition) to an open forest of park aspect with openings in which a grass-sedge ground cover is well developed (Fig. 16). The more open parts occupy depressions, places usually dominated by pin oak. Pin oak and swamp white oak may be here in small numbers, and may even be present in the understory. Such open white oak areas contain some of the typical shrubs and herbaceous plants of pin oak openings. More typically, the white oak forest is a closed community with an understory of fairly tolerant and tolerant species. Area 7 (Table 2) is such a white oak forest with an understory in which white oak is the most important species and shellbark hickory, black oak, beech, dogwood, serviceberry *(Amelanchier canadensis)*, elm, red maple, and swamp white oak are

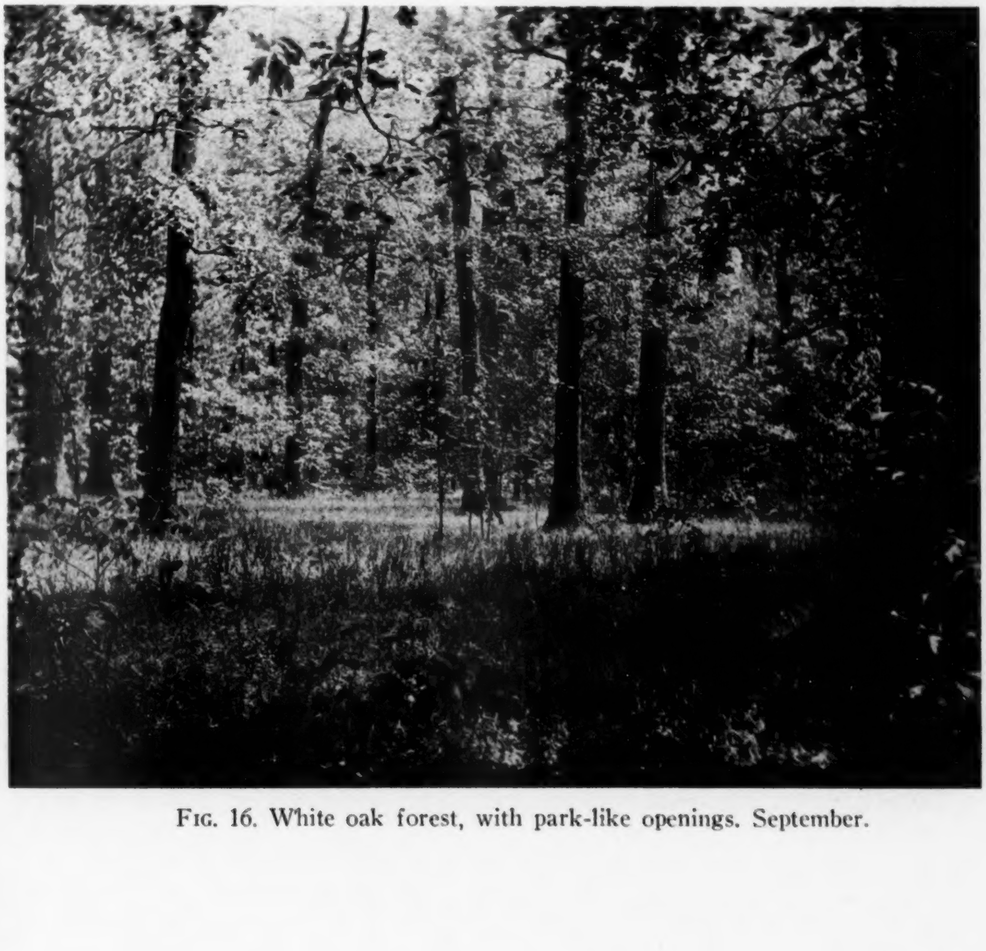

FIG. 16. White oak forest, with park-like openings. September.

also present (Fig. 17). In other areas successionally older, hickory and beech or beech are most important in the understory.

The Beech-Red Maple-Elm-Sweet Gum, Beech-Red Maple, and Beech-Red Maple-Elm Communities

The invasion of beech in the red maple, red maple-elm, or red maple-elm-sweet gum associes-segregates results in intermediate stages in which the constituent species are mixed in all proportions, or in some instances, in a forest in which beech reaches an importance amounting almost to dominance. The commingling of all species is illustrated by forest area 8 (Table 2)—within the finest virgin stand of mixed forest on the till plain (Figs. 10, 11, 13, 18A, 18B, 19, 21, 26, 29A, 29B). All gradations from the more open depressions (Fig. 11) and sweet gum swamps (Fig. 10) to the beech climax forest (Fig. 26) are discernible in this forest. Much of the forest is, however, a mixed stand of beech, red maple, elm, sweet gum, with locally, white oak, hickory and sour gum (Figs. 18A, 18B, 19).

Beech in wet places in these intermediate forest communities shows the adaptability of its root system and behaves as do the occasional beech trees in red maple depressions. Fine roots form a thick mat in the upper few inches of soil. These intermediate stages in which beech is prominent assume early the deep shade conditions characteristic of the climax stands. This, together

FIG. 17. White oak forest with understory of tolerant species. This is in area 7 (Table 2). November.

with root competition due to the superficial position of beech roots, acts to prevent the entrance of white oak in this sere. A selected plot in this community is shown in Fig. 14B; this plot is 150 feet from the plot of the red maple-elm-sweet gum associes-segregate shown in Fig. 14A and lies at a level 2½ feet above that plot.

FIG. 18 (A). A mixed forest with elm (left) and pin oak (right) in foreground and beech and white oak beyond; in forest area 8 (Table 2).
(B). Beech, red maple, elm, and sweet gum, constituents of intermediate stages, in a compact group in forest area 8 (Table 2).

FIG. 19. A mixed stand with beech, red maple, elm, sweet gum, and shellbark hickory; in area 8 (Table 2).

The undergrowth is made up of canopy species and occasional tulip trees, sugar maple and red oak. Spice bush *(Benzoin aestivale)* is an important shrub and introduces something of the climax aspect. The herbaceous plants are few. Mosses are much less conspicuous than in earlier stages.

Beech-White Oak-Sweet Gum, Beech-White Oak-Red Maple, and Beech-White Oak-Red Maple-Sweet Gum Communities

Beech-white oak-sweet gum or beech-white oak-red maple-sweet gum succeed the initial pin oak-red maple-elm-sweet gum associes; or, beech-white oak-sweet gum may develop from the pin oak-sweet gum, or even from the red maple-elm-sweet gum associes-segregate. The high crowns of sweet gum admit more light to the understory than do those of red maple and elm, hence the admixture of sweet gum in initial forest stages makes possible the later entrance of white oak in any succession in which sweet gum is initially present, even though pin oak may be absent.

Beech-white oak-red maple, developmentally, is derived only from the pin oak-red maple—a community of unusual occurrence. However, the beech-white oak-red maple community appears sometimes to succeed other initial stages in which red maple is important and pin oak absent (see Fig. 32). In such instances, it occupies positions intermediate between successions developing from unlike initial stages, as illustrated by Fig. 20. When in two adjacent depressions the initial stages are different, apparent inconsistencies in order of successional stages occur. A profile such as is represented by Fig. 20 (with the distribution of forest communities indicated by initials) illustrates

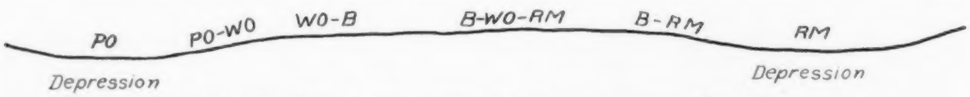

FIG. 20. Commingling of communities derived from unlike initial stages.

this point. Of all the communities represented, white oak-beech is successionally most advanced. Yet there is little reason to believe that white oak-beech will succeed the beech-white oak-red maple. Rather, both may in time give way to beech. Two successions are here in progress: (1) pin oak → pin oak-white oak → white oak-beech → beech and (2) red maple → beech-red maple → beech. An intermingling of communities occurs in the zone of contact resulting in the beech-white oak-red maple community which is not to be interpreted as a developmental stage following beech-red maple.

The beech-white oak-sweet gum and beech-white oak-red maple-sweet gum communities occur only in the southern half of the area, because of the limitation in range of sweet gum. The wide range of tolerance of sweet gum permits its continuance in succession to late intermediate stages. Statements made by Cheney (1929) concerning the extreme intolerance of this species are not applicable in the area under consideration. It does reproduce in the

FIG. 21. Large sweet gum trees in forest of intermediate successional stage. Large tree to right is 9 ft. 3 in. in circumference, b.h.

mixed forest of intermediate stages (see Fig. 22), there growing tall and slender and pushing up into the light (Fig. 21) and is never dominant in any forest in which it occurs, except in some relatively small areas of second growth stands.

The proportions of the dominants in these three communities may vary considerably. Other trees of the initial and earlier intermediate stages, as elm, pin oak, sour gum, and shellbark hickory, may be present. The undergrowth contains, in addition to the species of the canopy, Carpinus and an admixture of mesophytic species as dogwood, tulip tree, sugar maple, mulberry, wild cherry, and white ash. Elderberry *(Sambucus canadensis)*, papaw *(Asimina triloba)*, and spice bush *(Benzoin aestivale)* are often present. Among the few and usually scattered herbaceous plants are: ferns *(Aspidium noveboracense, Asplenium angustum, Onoclea sensibilis,* and *Botrychium obliquum)*, partridge berry *(Mitchella repens)*, pipsissewa *(Chimaphila maculata)*, red touch-me-not *(Impatiens biflora)*, May apple *(Podophyllum peltatum)*, and cucumber-root *(Medeola virginica)*. The soil here is looser than in earlier stages and generally covered with a light leaf litter.

A chart of a selected plot in the beech-white oak-sweet gum community (approaching beech-white oak) is shown in Fig. 22. This is within area 12 (Table 2).

C. Late Successional Stages

Late in successional development and with approach toward a climax stage, the number of forest communities decreases so that not more than two

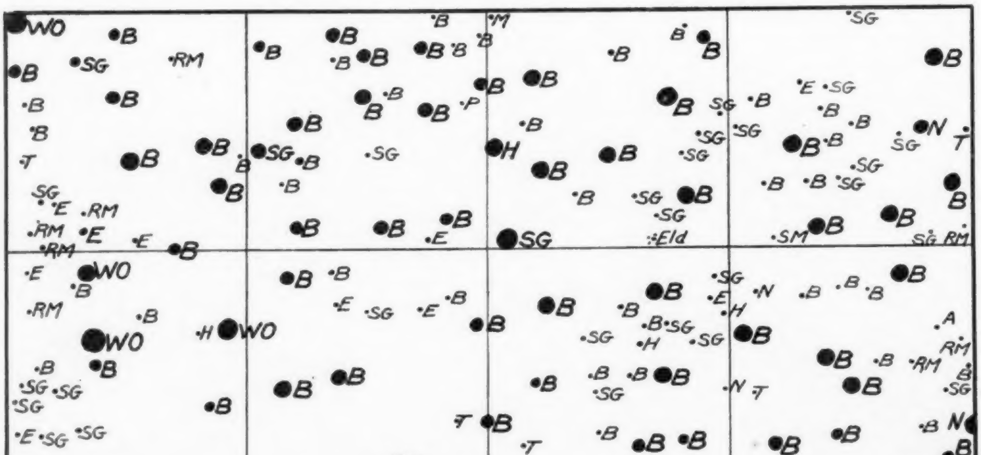

Fig. 22. Representative plot (130 x 200 ft.) in advanced stage of beech-white oak-sweet gum community; in forest area 12 (Table 2). (For key to symbols see p. 129.)

or three are recognizable: the white oak-beech associes, by far the most important; a variant of this, a forest of beech and white oak in which beech is dominant and white oak secondary; and a beech or beech-ironwood forest community. Each may ultimately develop into the beech climax forest, if dissection does not destroy the plain before the developmental series reaches its culmination.

White Oak-Beech Associes

A white oak-beech forest, with a scattering of the more hydrophytic species of earlier successional stages and of mesophytic species, is the most advanced stage in forest development reached over much of the till plain. In the associes as such white oak and beech in nearly equal numbers form about 90 per cent of the stand, with shellbark hickory, ash, black and red oak, and sour gum as secondary species (Fig. 23). However, in any given forest tract the inclusion of small groups of more hydrophytic species reduces the percentage of white oak and beech from 90 to 60 or 75. Pin oak, swamp white oak, èlm, and red maple occupy the depressions or shallow ravine heads and are remnants of earlier successional stages. Areas 14 to 17 (Table 2) are representative of the white oak-beech forest; for one area, no. 14, the distribution of secondary and hydrophytic species is illustrated in the transect, Fig. 30. In the best examples of the white oak-beech forest (as area 17), the aspect from a distance is of a white oak forest. This tree dominates because of its greater size and height, here reaching its largest size, 10 to 14½ feet in circumference, b.h. In such forests (Figs. 23, 24) beech, though

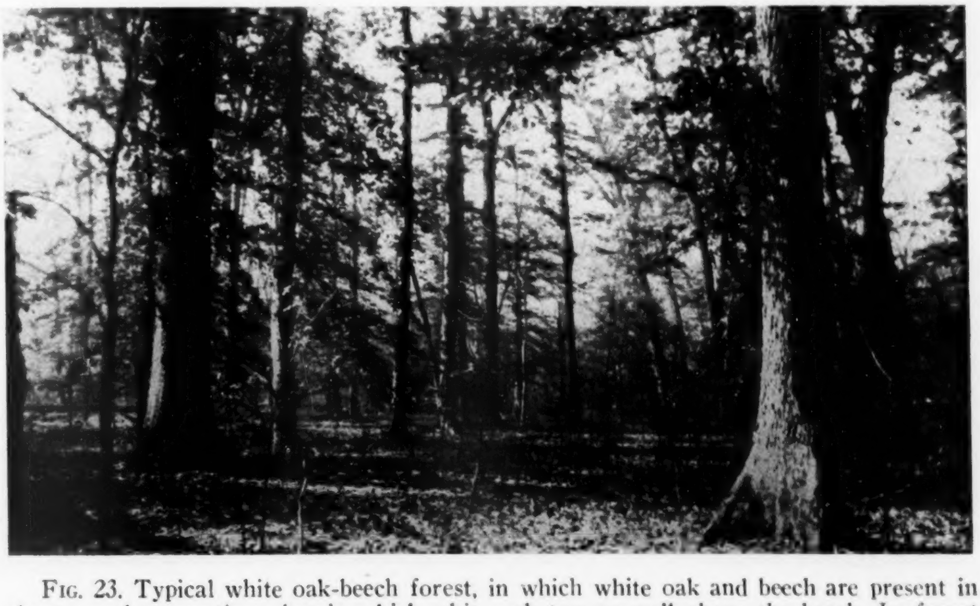

FIG. 23. Typical white oak-beech forest, in which white oak and beech are present in about equal proportions, but in which white oak towers well above the beech. In forest area 17 (Table 2.)

large, forms something of a lower story beneath the white oak. Generally, in the white oak-beech associes, beech varies from year old seedlings to trees 10 feet in circumference. Locally, beech is dominant (Fig. 25) and in these places is larger than elsewhere; locally white oak, even numerically, dominates (Fig. 24) where beech trees are smaller. The largest beech trees occupy the oldest topographic situations—the edges of the almost imperceptible ravines and the ridges. Hydrophytic herbaceous species have disappeared; *Ilex verticillata* and *Viburnum pubescens* var. *indianense* may be present, though never abundant nor vigorous; more mesophytic species, especially spice bush, become abundant. The herbaceous layer is still poor; a very few common species of mesophytic forests have entered, as *Podophyllum peltatum*, *Phlox divaricata*, and rarely *Eupatorium urticaefolium*. The best areas of the white oak-beech forest (as far as canopy is concerned) are badly grazed by hogs and very little undergrowth remains.

Beech is reproducing much more abundantly than white oak; the indication from the composition of half-grown trees is that a beech forest will in time succeed the white oak-beech forest. This is substantiated by the greater dominance of beech in situations in which succession has progressed most rapidly.

The typical white oak-beech forest is one in which these two species are present in about equal proportions, with beech becoming dominant as succession progresses. The forest with beech a dominant is a transition phase between the white oak-beech associes and the climax beech forest. However, in some areas a beech-white oak forest occurs which seems never to have had a high percentage of white oak.

FIG. 24. White oak-beech forest where white oak numerically exceeds beech; here beech trees are smaller than in the typical white oak-beech associes. In forest area 17 (Table 2.)

Sugar maple may be present in the understory of the white oak-beech forest or codominant with beech in that layer. This is always true at the margin of the till plain and on the gentle slopes of stream headwaters. This points to the possible terminal—though not climax—position of the white oak-beech associes. A forest community of the till plain will be replaced by one of the slope series. This is indicated by zonations in which the white oak-beech forest of flats passes almost imperceptibly into a beech-sugar maple-white oak forest of slopes, or the beech-white oak forest into a beech-sugar maple slope forest (see transect, Fig. 34). This is a step toward the regional climax, but not a stage in the developmental succession in progress here. The developmental succession—white oak-beech → beech—is clearly indicated in many places, both by understory and zonation.

Beech or Beech-Ironwood Associes

Beech enters early in successions in which red maple is important in the initial stages. This results in the early dominance of beech, at first with red maple in the beech-red maple intermediate stage, later in a forest in which red maple still persists, although it is unimportant. This beech forest—a late developmental succession—white oak-beech → beech—is clearly indicated in —shares with other developmental stages of the till plain successions, the

FIG. 25. Beech dominates in local areas in the white oak-beech forest; here beech trees are larger than in the mixed parts of the stand. Figs. 24, 23, and 25, all from the same forest area, indicate clearly the successional development in progress.

features imparted by the admixture of somewhat hydrophytic herbs and the moss or moss-lichen mats about exposed tree roots. Beech roots here have the superficial habit which characterizes them throughout all hydric stages. In many places, ironwood *(Carpinus caroliniana)* is an important or dominant member of the understory. Such communities frequently occupy the indefinable depressions at ravine heads; the soil seems usually to be the Blanchester silt loam. A change to less wet conditions results in a change in understory, if not in canopy, and leads to the establishment of the beech climax forest, between which and the beech-red maple forest, this community is transitional.

D. Beech Forest: A Physiographic Climax or Subclimax

A beech forest is the usual type near the margins of the upland plains, where the beginning of dissection has lowered the water table slightly, on smaller remnants of the till plain, on the yellowish Rossmoyne silt loam, and locally on dark soil in the undissected plain. The beech forest contains fewer species than most of the other forest communities of the till plain, and is characterized by the marked dominance of beech, which comprises 80 to 90 per cent of the forest stand (Figs. 25, 26). Forests having much the aspect of this beech forest have been at times produced by the cutting of white oak in the white oak-beech associes (Fig. 27); this should not be confused with the true beech association. Some areas of the beech association are succes-

Fig. 26. Beech forest—the physiographic climax or subclimax of forest development on the till plain.

sionally related to the white oak-beech forest and represent the final dominance of beech, the most tolerant species of the forest of the till plains. Other areas appear not to have passed through a white oak-beech stage, but rather to represent the culmination in development in the red maple succession. These are apt to contain remnants of red maple, whose wide range of tolerance makes it possible for it to persist through the entire succession in which it is originally prominent. Areas 18 and 19 (Table 2) show the composition of the beech association; area 19 lies closer to the margin of the upland plain, hence has felt more the influence of dissection and contains fewer red maples.

The understory of the beech forest differs from all other communities in the greater prominence of those mesophytic species which are common in the regional climax. Beech is always prominent in the understory, and with it sugar maple, white ash, and dogwood, which emphasize the relationship to the mixed mesophytic forest. Papaw, spice bush, elderberry, and Carpinus are also usually present. White oak may be represented in the understory in less dense places and points to the appearance of white oak in the mixed mesophytic forest of the slopes.

The herbaceous layer is poor, but contains a few of the plants of the mixed mesophytic forest as *Eupatorium urticaefolium, Circaea lutetiana, Amphicarpa monoica, Podophyllum peltatum,* and *Viola eriocarpa.* Virginia creeper

FIG. 27. Beech forest produced by the cutting of white oak from a white oak-beech associes. Such forest closely resembles the beech climax association.

(Psedera quinquefolia), which is seldom seen in wet flats, appears. *Impatiens biflora*, present in every shaded moist place in the flats, persists to the margin of the plain where it gives way to *Impatiens pallida*.

This beech forest marks the most advanced successional stage possible on the till plains. When this stage is reached on flats more or less remote from drainage lines, beech dominates in the understory as well as in the canopy and the forest continues to reproduce itself as long as topography remains unchanged. The wet and acid soil prevents the entrance of other tolerant species. The beech association is, therefore, a sub-climax or physiographic climax, a climax in which beech alone dominates, a condition contrasting with the regional or climatic climax, in which the dominance of beech is much less marked and is shared with other tolerant mesophytic species.

E. Forest of Ravine Slopes: The Regional or Climatic Climax

The forest of ravine slopes is not to be considered as a part of the forest of the undissected till plain. However, in order to emphasize the immediate effects of dissection it is desirable to contrast the forest of flats with the adjacent slope forest.

The transition from the beech forest of upland to the mixed forest of slopes is fairly abrupt, the amount and suddenness of the change dependent on the abruptness of the slope.

The transect, Fig. 34, demonstrates the abruptness of change from the forest of the flat to that of ravine slopes where ravines are rather gully-like. It also emphasizes the fact that the effects of dissection do not extend far into the plain beyond the immediate slope of the ravine.

Area 20 (Table 2) is a continuation of forest area 19 and shows the change in composition resulting from dissection. All hydrophytic tree species are eliminated; a number of the characteristic species of the mixed mesophytic forest enter. In this instance, tulip and sugar maple are most important. The number of species in the slope forest is greater than that of adjacent flats, and beech at once loses its complete dominance.

The change in ground cover is even more marked than is the change in canopy or forest understory. Instead of the meager herbaceous vegetation, a rich and varied flora is seen including a large variety of species never seen on the flats. Here are *Asplenium angustifolium, Cystopteris fragilis, Phegopteris hexagonoptera, Botrychium virginianum, Uvularia grandiflora, Smilacina racemosa, Trillium grandiflorum, Orchis spectabilis, Aplectrum hyemale, Pogonia trianthophora, Actaea alba, Caulophyllum thalictroides, Sanguinaria canadensis, Stylophorum diphyllum, Asarum canadense, Panax quinquefolium.* The forest is essentially one of the mixed mesophytic type—the regional or climatic climax for southwestern Ohio.

Area 21 (Table 2) shows the composition of the mixed mesophytic forest

of the slopes of a ravine cutting through the till plain. For the sake of comparison the average composition, based on a number of areas of mixed mesophytic forest of the more deeply cut valley slopes contiguous to the flats, is shown in the last column of Table 2. The absence of all of the species of earlier successional stages of the flats (except locally of Nyssa which may occur in any type of forest); the importance of such species as sugar maple, tulip, sweet buckeye, and basswood, and the presence of a considerable number of other mesophytic species distinguish this, the regional or climatic climax forest, from the subclimax or physiographic climax of the undissected till plain.

F. TRANSECTS

The series of transects, Figures 28, 30, 32, 34, demonstrate the close correlation between community and topography. The importance of soil water as controlled by topography is evident. In all cases, no cutting has been done within the area of the transect; the forest is primary and as far as canopy is concerned, virgin, though in some instances grazing has affected the ground cover.

Contours are shown when the profile accompanying transect is not sufficient to depict topographic features. pH values of soils in the transects are given beneath the profile and the location from which soil was taken is shown by a rectangle in the transect. Each of these transects has been referred to in connection with the treatment of the respective communities. The specific features of each are given here, together with the key to the letters and symbols used on all charts and transects. Relative sizes of trees are indicated by size of dots; stumps, if present, by crossed instead of solid circles. Tree roots when on the surface of the ground are plotted. Initial letters are printed smaller for saplings than for canopy trees. Clumps of shrubs are shown by dots surrounding the letter symbol. Patches of herbaceous plants or ground shrubs, when prominent, are shown by symbols surrounding the name.

ABBREVIATIONS AND SYMBOLS

A—white ash, *Fraxinus americana*
Al—green ash, *Fraxinus pennsylvanica* var. *lanceolata*
Am—serviceberry, *Amelanchier canadensis*
B—beech, *Fagus grandifolia*
Blackb—blackberry, *Rubus frondosus*
C—red cedar, *Juniperus virginiana*
Car—ironwood, *Carpinus caroliniana*
Cr, Crat—*Crataegus sp.*
D—dogwood, *Cornus florida*
E—white elm, *Ulmus americana*
Er—red elm, *Ulmus fulva*
Eld—elderberry, *Sambucus canadensis*
Goosb—gooseberry, *Ribes Cynosbati*

Grape—wild grape, *Vitis cordifolia*
H—shellbark hickory, *Carya ovata*
Ha—white-heart hickory, *Carya alba*
Hc—bitternut hickory, *Carya cordiformis*
Hp—pignut hickory, *Carya glabra*
Ilex—winterberry, *Ilex verticillata*
M—mulberry, *Morus rubra*
RM—red maple, *Acer rubrum*
SM—sugar maple, *Acer saccharum*
N—sour gum, *Nyssa sylvatica*
BO—black oak, *Quercus velutina*
PO—pin oak, *Quercus palustris*
RO—red oak, *Quercus rubra*
ShO—shingle oak, *Quercus imbricaria*
SWO—swamp white oak, *Quercus bicolor*
WO—white oak, *Quercus alba*
O—hop hornbeam, *Ostrya virginiana*
P—wild cherry, *Prunus serotina*
Pa—papaw, *Asimina triloba*
P. ivy—poison ivy, *Rhus Toxicodendron*
Rasp—raspberry, *Rubus occidentalis*
Rb—redbud, *Cercis canadensis*
Rose—climbing rose, *Rosa setigera*
Rosa car.—swamp rose, *Rosa carolina*
Sas—sassafras *Sassafras variifolium*
Sbn—*Smilax Bona-nox*
Sp, Spice—spicebush, *Benzoin aestivale*
Syc—sycamore, *Platanus occidentalis*
SG—sweet gum, *Liquidambar styraciflua*
T—tulip tree, *Liriodendron tulipifera*
V—black haw, *Viburnum prunifolium*
Vd—arrow-wood, *Viburnum pubescens* var. *indianense*
W—walnut, *Juglans nigra*
oblique dashes—poison ivy, *Rhus Toxicodendron*
single vertical dashes—wood reed-grass, *Cinna arundinacea*
groups of vertical dashes—*Carex spp.*

A transect 200 feet long and 75 feet wide (Fig. 28) in a depression in an ungrazed virgin forest in Highland County (area 8 of Table 2) passes from an advanced red maple-elm-sweet gum stage through beech-red-maple-elm-sweet gum and beech-white oak. There is a rise of only one foot in 150 feet in this transect. The white oak is probably older than the other trees—except perhaps some of the red maples. Sedges and grass *(Cinna arundinacea)*, *Onoclea sensibilis*, and *Phlox maculata* var. *odorata* are the most important herbaceous plants of the open forest of the depression; other species present are *Chelone glabra*, *Ranunculus hispidus* var. *falsus*, *Polygonum arifolium*, *Solidago rugosa*, *Agrimonia parviflora*, *Scutellaria lateriflora*, *Boehmeria cylindrica*, *Lobelia cardinalis*, *Viola cucullata*, *Thalictrum*

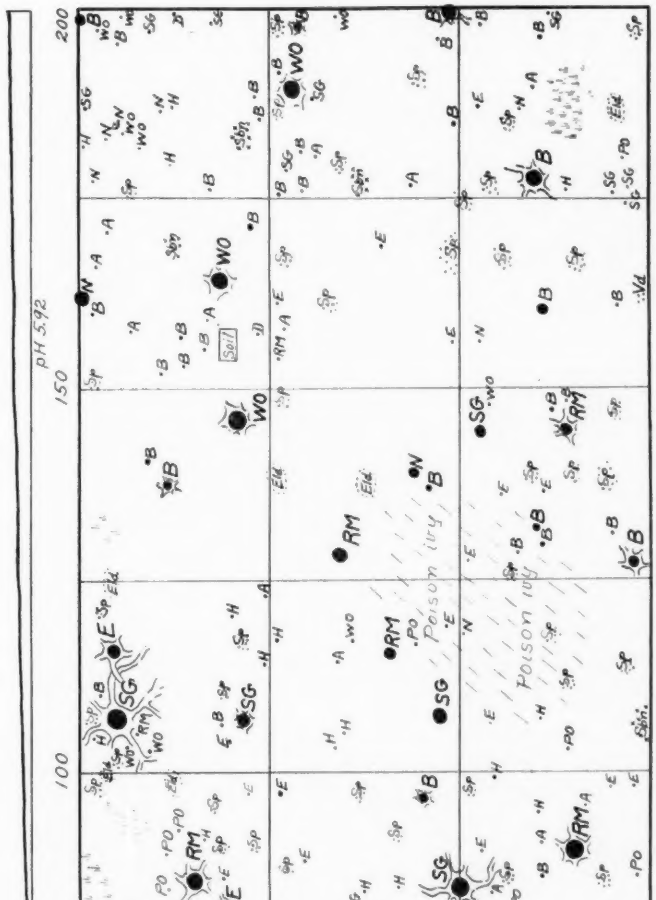

FIG. 28. Transect 200 feet long and 75 feet wide from red maple-elm-sweet gum through beech-red maple-elm-sweet gum to beech-white oak.

FIG. 29 (A). Red maple, elm, and sweet gum in lower portion of area of transect, Fig. 28. October.

(B). Beech, elm, and two sweet gums, with white oak and beech beyond; slope and rim of depression traversed by transect, Fig. 28. October.

purpureum, Penthorum sedoides, Mimulus ringens, Ludvigia palustris, Impatiens biflora, and *Ilysanthes dubia*. Shrubs in the depression include *Ilex verticillata, Viburnum pubescens* var. *indianense, Benzoin aestivale, Smilax Bona-nox*, and *Rhus Toxicodendron*. The composition of the understory is shown in the transect; species of the initial forest stages continue to dominate. In the beech-red maple-elm-sweet gum part of the transect, poison ivy becomes much more prominent; elderberry enters and spicebush becomes more abundant. The sedges and grass and most of the herbaceous plants mentioned above drop out. Beech becomes more plentiful in the understory. In the beech-white oak part, all trees of the initial stages are absent in the understory except hickory and an occasional sweet gum. Dogwood has appeared. Figures 11 and 29A, 29B show the aspect of the vegetation. Other parts of the same forest tract are illustrated by Figures 10, 13, 18A, 18B, 19, 21 and 26.

A transect 1,200 feet long and 50 feet wide (Fig. 30) traversing areas 1 and 14 (Table 2) demonstrates the sequence of communities in the pin oak → white oak → beech succession. The total relief is 4 ft. 8 in. For 200 feet the transect passes through a typical pin oak opening with a continuous sedge ground cover except under the one beech tree. *Ranunculus hispidus* var. *falsus, Cardamine bulbosa*, and *Phlox maculata* var. *odorata* are scattered among the sedges. *Rosa setigera* is the only shrub present. There are very few small trees. On the slopes of the depression, still within the pin oak consocies, saplings become abundant and point to the formation of a denser stand and the elimination of the sedge ground cover. A transitional belt of hickory (*C. ovata* and *C. alba*) with black oak intervenes between the pin oak and the white oak-hickory stages; this does not have a sedge ground cover. Beech becomes prominent in the understory of the white oak-hickory forest, continuing through the white oak-beech into the beech area. The last 150 feet passes down into another but shallower depression occupied by pin oak with an admixture of black oak and white oak. Saplings are abundant but not yet large enough to shade out the sedges. Figure 31 A, B, C, D shows the aspect of communities along the transect.

The influence of broad shallow ravines with old streams not yet rejuvenated is demonstrated by a transect 1,050 feet long (Fig. 32) crossing such a ravine and the adjacent flat and ending in a very shallow depression. The total relief is 16 feet. The ravine flat, in which is a shallow anastomosing stream, is occupied by an elm-pin oak community (20 to 80 ft.); the adjacent ravine slopes by white oak with sugar maple and dogwood prominent in the understory, a mesophytic character correlated with dissection of the plain (80 to 240 ft.). A white oak-beech community with beech, sugar maple, and dogwood in the understory occupies the very gentle upper slopes and margin of the plain (240 to 550 or 600 ft.). On the flat, the forest is beech-white

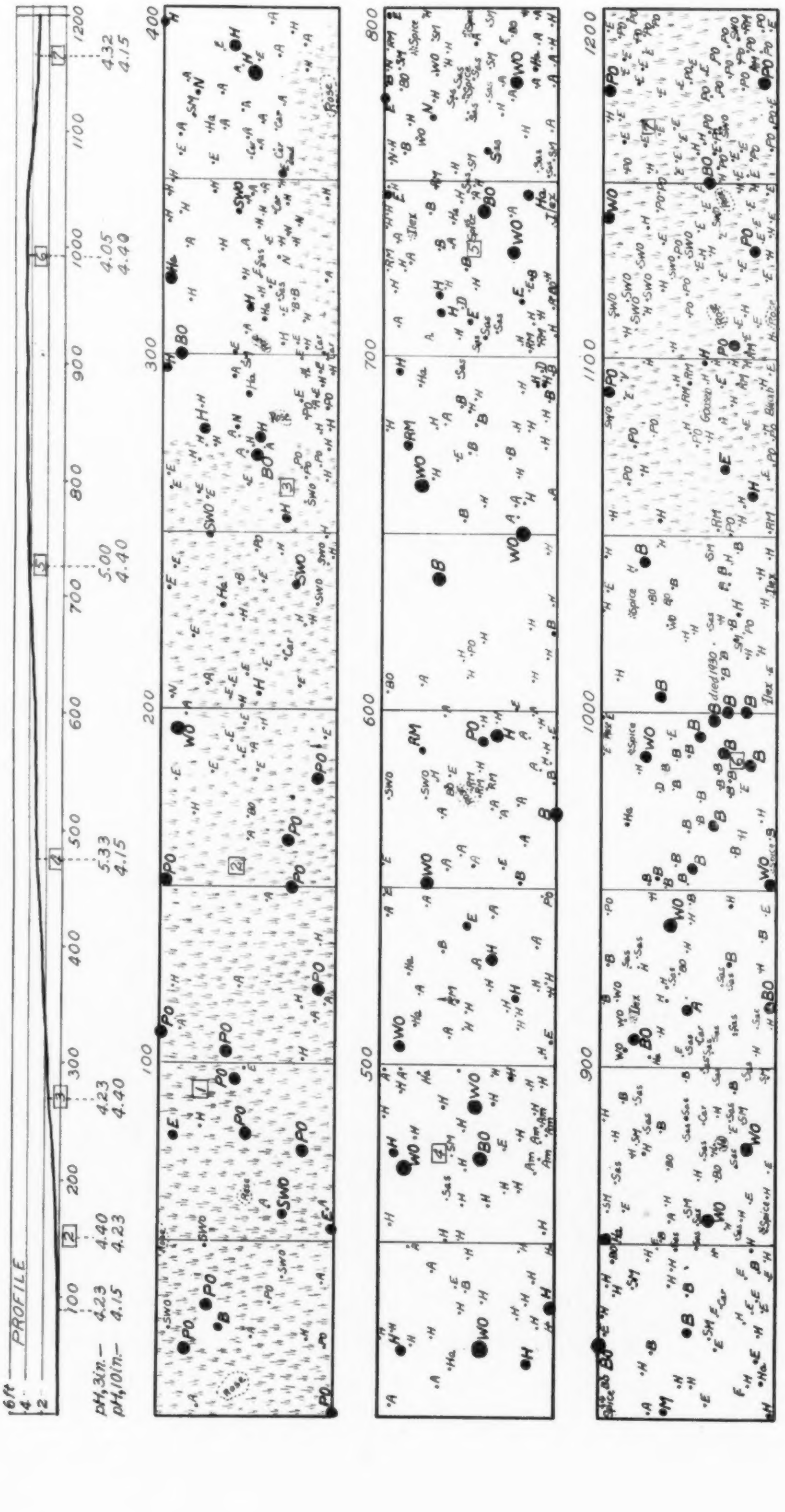

FIG. 30. Transect 1,200 feet long and 150 feet wide illustrating the pin oak → white oak → beech succession.

FIG. 31. Forest communities along transect, Fig. 30.
(A). Pin oak-sedge area with large shellbark hickory to left.
(B). White oak with black oak (right) and shellbark hickory (center right).
(C). White oak-beech.
(D). Beech.

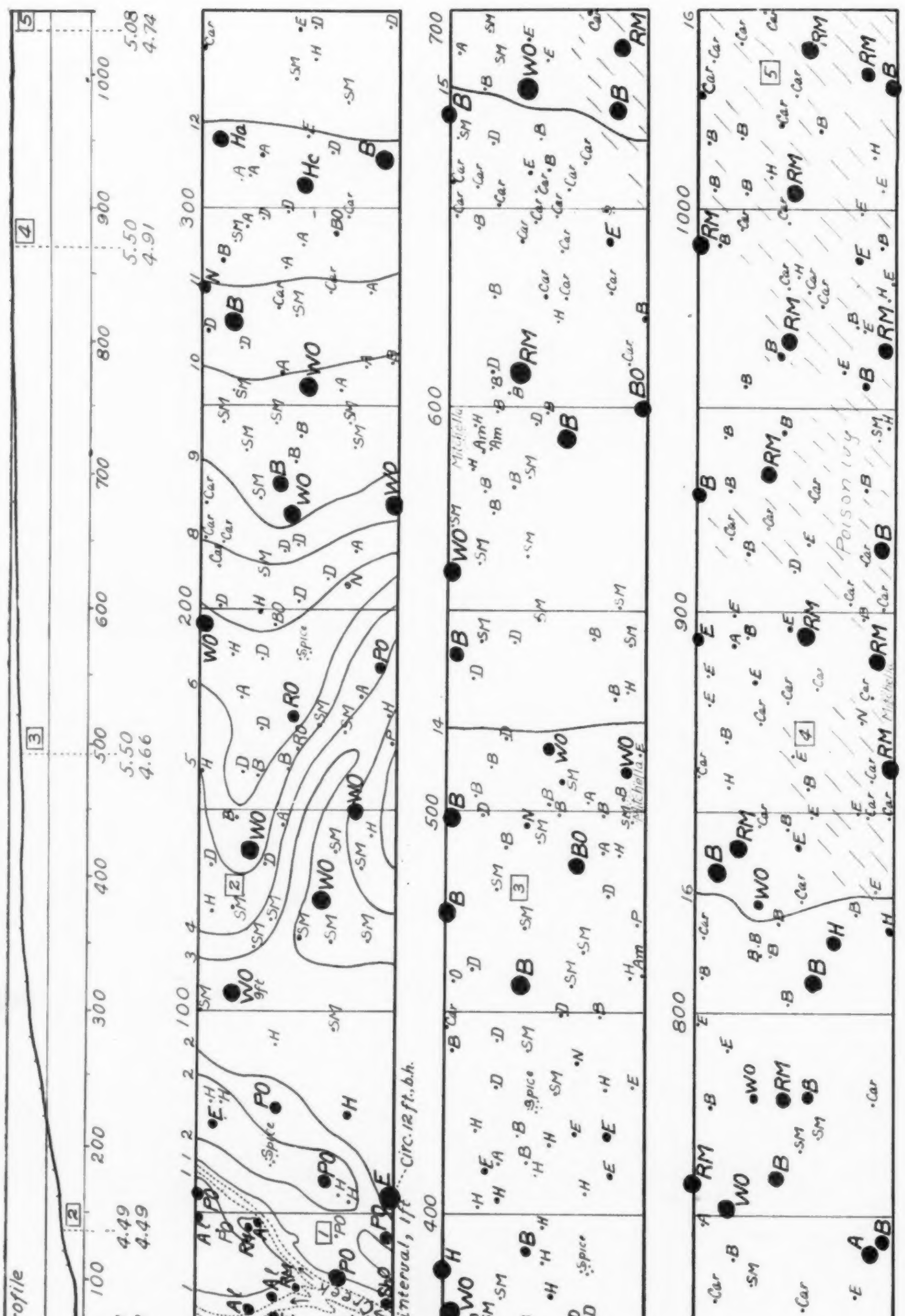

FIG. 32. Transect 1,050 feet long and 50 feet wide to show influence of broad shallow ravines.

FIG. 33. Aspect of forest along transect, Fig. 32. November.
(A). In swamp forest of shallow ravine flat.
(B). In white oak-beech at top of slope.
(C). In beech-red maple of shallow depression.

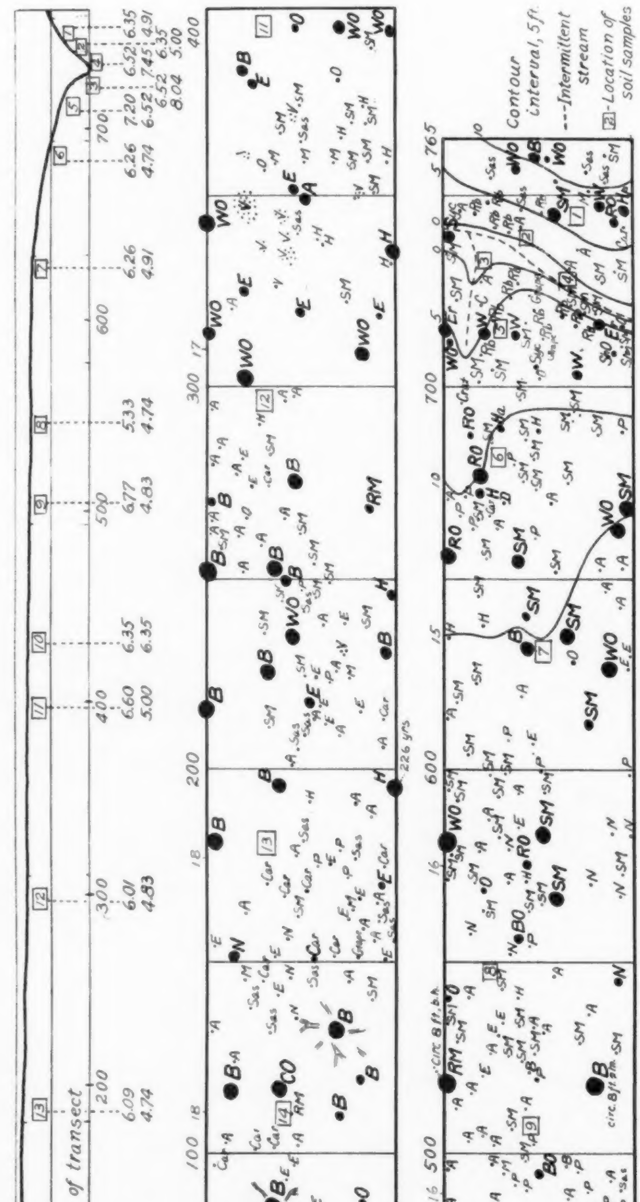

FIG. 34. Transect 765 feet long crossing a V-shaped ravine cut in till plain.

oak-red maple with beech and Carpinus most prominent in the understory and occasional Amelanchier; poison ivy forms an almost continuous ground cover; *Mitchella repens* is present (600 to 800 ft.). Beech-red maple, with beech and Carpinus in the understory, occupies the wet flat (800 to 1,050 ft.). This transect illustrates the intermingling of communities of two different successions, as discussed in connection with Figure 20. The aspect of communities of this forest is shown by Fig 33 A, B, C.

More pronounced stream dissection with V-shaped ravines of eroding streams, permits the entrance on the ravine slopes of a variety of trees of the mixed mesophytic forest. A transect (Fig. 34) crossing such a ravine which is cut 16 feet below the adjacent plain shows the influence of dissection on the forest of the flat and the nature of the slope forest. The beech-sugar maple forest of the slope (with other mesophytic species) changes abruptly to a beech-red maple forest just back of the margin of the flat. Less than 600 feet from the stream beech is of the swamp forest type with roots spread upon the surface of the ground and 700 feet from the stream a depression only 6 inches below the level of the plain contains such swamp forest species as pin oak and swamp white oak. It will be noted that the soils of the ravine slopes are for the most part circumneutral; those of the flat and slight depression acid; and that the most acid soils are those of the depression.

IV. SECONDARY VEGETATION

The secondary vegetation of the till plains is made up of herbaceous and shrub meadow communities and forest. Locally, small and shallow ponds, frequently intermittent, introduce communities of hydrophytes (Fig. 35). Many of these ponds are partly artificial and were made by the deepening of depressions which doubtless originally contained ponds.

Ponds and Wet Meadows

In the intermittent and shallow ponds few aquatics occur. Amphibious and swamp plants are most abundant and include:

Eleocharis obtusa
Eleocharis capitata
Scirpus cyperinus
Scirpus atrovirens
Carex (species of pin oak openings)
Juncus effusus
Juncus marginatus
Juncus brachycarpus
Juncus acuminatus
Leersia oryzoides
Glyceria septentrionalis
Alisma subcordatum
Lophotocarpus calycinus
Sagittaria latifolia
Typha latifolia (very rarely)
Ranunculus laxicaulis
Ranunculus pusillus
Penthorum sedoides
Callitriche heterophylla
Ludvigia palustris
Mimulus alatus

FIG. 35. Shallow pond in till plain around which Eleocharis and Juncus, Carex and Scirpus, *Rosa setigera* and *R. carolina,* and pin oak form successive zones leading to the primary forest which is close by and to which the large white oak on the right belongs.

Only a few of these are limited to ponds or pond margins. The marginal swamp plants of ponds may be the pioneers of wet flats. These secondary swamps contain many plants not seen in primary forest openings; these are the common and rather widespread hydrophytes. A few species only, as *Lophotocarpus calycinus,* the two species of Ranunculus, and some of the sedges and rushes, are in this general region limited to the till plain. These occur in primary as well as secondary areas.

Meadow Communities

Meadow communities are extensive. Some have occupied land formerly tilled; others have followed cutting on land never agriculturally utilized. Meadows on the yellowish Rossmoyne silt loam, on the dark Blanchester silt loam, and on the white clay or Clermont silt loam differ decidedly from one another. On the Clermont silt loam the greatest variety of species is seen and only on this soil do the more characteristic plants of the till plain become abundant.

Meadows dominated by *Andropogon virginicus* are the general type on the Rossmoyne silt loam. Such meadows usually contain, in addition to the Andropogon, a few other grasses *(Agrostis perennans, Eragrostis pectinaceus, Aristida gracilis, A. purpurea), Polygala sanguinea, Solidago nemoralis,* and *Gnaphalium polycephalum.* In areas recently tilled the latter two plants may dominate. Some shrub and tree invasion is usually evident; dewberry *(Rubus trivialis)* and blackberry *(Rubus frondosus)* are the common shrubs; Sassafras is the most abundant tree invader; with it may be a number of other species as white elm, hickory, and sour gum.

The meadows of the Blanchester silt loam areas are without characteristic plants; they are usually weedy ruderal communities which may contain some swamp plants.

The white clay or Clermont silt loam supports herbaceous and shrub meadows floristically distinct from other communities. Recently abandoned tilled land is usually occupied by Aristida, either *A. gracilis* or *A. purpurea* (Fig. 36). Land which has not been tilled or long-abandoned tilled land adjacent to untilled land is occupied by a variety of herbaceous plants; grasses and sedges are not dominant except in depressions where the wet meadow vegetation prevails. More abundant or characteristic herbaceous plants are:

Aspidium thelypteris
Panicum clandestinum
Scirpus cyperinus
Lilium canadense
Habernaria peramoena
Spiranthes cernua
Polygonum sagittatum
Apios tuberosa
Viola cucullata
Viola lanceolata
Ludvigia alata
Rhexia virginica
Oxypolis rigidior
Sabatia angularis
Gentiana Saponaria
Mimulus alatus
Chelone glabra, and var. *elongata*
Lobelia cardinalis
Eupatorium perfoliatum
Eupatorium maculatum
Solidago rugosa
Solidago canadensis
Aster vimineus
Aster umbellatus
Coreopsis tripteris

In open places in the meadow the ground is covered by a varied growth of Cladonia (*C. furcata, C. pyxidata, C. verticillata, C. mitrula, C. cristatella, C.*

FIG. 36. The first step in the re-occupation of tilled Clermont silt loam: *Aristida gracilis* meadow. To the left, an old secondary oak forest; in the distance, an area of primary forest of the till plain.

subcariosa, and others). Mosses, especially *Polytrichum ohioense*, are common; locally Sphagnum is important.

The herbaceous meadow community of the white clay always contains an admixture of shrubs or is nearly supplanted by a shrub community. Here are found in greatest abundance, the "characteristic shrubs" of the till plain (except *Viburnum pubescens* var. *indianense*), as well as other shrub species:

Cephalanthus occidentalis
Cornus obliqua
Cornus racemosa
Corylus americana
Hypericum prolificum
Ilex verticillata
Pyrus melanocarpa
Rosa carolina
Rosa setigera
Rubus frondosus
Rubus trivialis
Salix discolor
Spiraea alba
Spiraea tomentosa
Vitis labrusca

Locally, in the wettest places, Cephalanthus is dominant. The roses, *R. carolina* and *R. setigera*, frequently dominate large areas (Fig. 37). *Spiraea tomentosa* is, in many places, the most important shrub and may nearly supplant the other species.

Tree invasion of the mixed herbaceous meadow and of the shrub meadow of the white clay is similar. The trees of the initial stages of primary forest

are the important invaders, though in many places, particularly in the denser shrub meadows, little invasion is taking place.

Secondary Pin Oak Forest

Pin oak in pure or almost pure stand covers a large part of the area now in forest and is by far the most important type of secondary forest. Such stands vary in age from but a few years to 60 to 70 years (Fig. 37). Twenty years ago numerous young stands were springing up; today, few areas are returning to pin oak. This change is due to ditching, the effects of which have become much more pronounced in the last decade. In this respect, the Indiana area of Illinoian drift contrasts strongly with the Ohio area. There, young stands of pin oak or sweet gum are frequently seen. Less effort has been made there to utilize the land; roadside and field ditching is not as extensive and consequently the water table is higher. Thus conditions are still favorable for the invasion of the more hydrophytic trees of initial primary forest stages and unfavorable to the invasion of such intolerant tree species as sassafras.

Where secondary pin oak forms a closed stand it eliminates almost all the herb and shrub species of the meadows. A few sedges, an occasional straggly Ilex or rose, are all that remain of the earlier vegetation. Poison ivy is usually the dominant ground cover, forming a shrub layer 1 to 3 feet in height.

FIG. 37. Secondary sedge meadow invaded by wild roses (*Rosa setigera* and *Rosa carolina*). Secondary stand of pin oak about 60 years of age beyond.

Irregular invasion by pin oak, leaving small more or less open spots, allows the meadow and shrub species to persist. Such places are almost identical with the pin oak openings of primary areas, and in some places where surroundings furnish no evidence, cannot with certainty be distinguished from primary areas.

Crowded stands of pin oak become very tall. With dying off of all lower branches and a greatly elevated canopy more light is admitted and the understory becomes more varied. The secondary pin oak forest 60 to 70 years old is very similar to the pin oak consocies of the primary vegetation except that it occupies more extensive continuous areas (Fig. 38). Indications from understory are that it will be succeeded by a mixed forest similar to that which follows in primary succession.

Secondary Sweet Gum Forest

Locally, and only in the southern part of the area, sweet gum is the most important tree invader. Such stands are few, but are mentioned here, because in the Indiana area sweet gum shares with pin oak in importance in young and middle aged secondary forests.

Red Maple Groves

Red maple, or red maple and elm, with or without pin oak are the most important trees in secondary stands about the indefinable ravine heads of the

FIG. 38. Interior of old second growth stand of pin oak.

flats and in areas of Blanchester silt loam generally. Here, too, secondary succession appears closely to parallel the primary.

Secondary vegetation of the till plain is important, ecologically, because it is here that many of the most characteristic plants among the herbs and shrubs—those of high light requirements and hence of early developmental stages—find growth conditions most favorable. In these secondary areas they have become abundant and the vegetation is suggestive of probable early stages of the primary successions. Their behavior in the meadows and in the redeveloping forests and forest openings is of value in reconstructing the successions of these glacial plains.

V. THE SUCCESSIONS RECONSTRUCTED

The development of vegetation on the Illinoian till plains began soon after the recession of the Illinoian ice sheet. Changes in climate and in habitat since that time and the reactions of invading plants have directed a series of climatic successions with their included lesser successions. Probably at no time since the first invasion of plants onto the new glacial plain has a primary bare area been exposed. The vegetation of today is the result, not alone of factors operative today, but also of the influences effective during the earlier periods of vegetational occupancy of this area.

Originally the habitat was probably a very slightly undulating wet plain dotted with shallow pools. The soil was a calcareous drift. Into this, the pioneers of the post-Illinoian clisere invaded. Continued invasions, the migrations instituted by the changing climates of the Wisconsin glacial age, and changing environment directed a progression of vegetation. Gradual leaching of the upper part of the drift, soil formation, the action of organic acids in water-logged and poorly aerated soils, and the reactions of vegetation continued, producing the acid soils of 100 or even 50 years ago. Then man started his modification of the environment—by cutting, by plowing, and most of all by ditching and draining.

In the original vegetation, hydrophytes must have been more or less prominent. The hydrarch succession may have resembled the present secondary hydrarch succession. Or, bogs may have prevailed in deeper depressions, and bog successions and gradual filling of depressions followed. On flats, lichens and mosses were doubtless pioneers—a condition repeated locally in the secondary meadows. Herbaceous and shrub species, including at least a part of those which now make up the flora of secondary meadows, probably early became prominent. These post-glacial meadows doubtless contained a large number of species of more northern range than now exist here—for plants of the earlier migratory waves must have made up these communities. Some have persisted (Braun, 1928, and 1935a); other more southern species have entered, so that, while throughout the progress of the great

climatic successions in this area, there were meadow communities and still are, the composition of these communities has continually been changed by the influx of southern invaders.

The period of conifer dominance, amply demonstrated by Sears (1930) on the youngest (Wisconsin) drift plains of Ohio, may never have been effective here. No evidence of such occupancy remains, either on the Illinoian till plain or along its margin.

Deciduous forest invasion, coincident with and dependent on the northward migration of deciduous forest species, must have been attended by the establishment of forests of the first invading species which found the more or less hydrophytic conditions suitable. The number of such species is limited. They must have been species which now range far northward. Some of the poplars, probably *P. tremuloides*, *P. grandidentata* and others, willows, and birch may have been among the first invaders. Occasional small groves of aspen and popple are found on these flats, the aspen always associated with some of the characteristic shrubs, the Spiraea, Ilex, etc.; these may be secondary invaders, or they may be relic species. *Salix discolor* is generally scattered over the area. Of the present pioneer tree species, red maple and white elm extend farther north than do the other species. This, together with the greater mobility of their propagules, suggests that these species may have preceded others of the present species. Such depressions which could, because of lesser depth, be first invaded by trees, would probably have been occupied by these species. Hence the first reactions of forest vegetation upon habitat would be of these species. Melin (1930) has demonstrated that different types of leaf litter decompose differently and yield different amounts of nitrogen. The soil of those depressions first occupied would have been modified by the earliest invaders. Later entrants, as pin oak, would then have found some areas already occupied and some soils modified by forest litter. Present differences in soil types of depressions—the white Clermont silt loam in some and the dark Blanchester silt loam in others—are due in part at least to the influence of past vegetation. The latest entrant among the trees of initial forest stages is sweet gum, a southern species still extending its range, and at present general only in the southern half of the area.

In depressions in primary vegetation areas, succession has reached only the first stages of tree invasion; such communities are still open, remnants of meadow and shrub species remain, and the wide spacing of the trees permits the continued entrance of pioneer tree species. In some, the large amount of sweet gum in the understory points to a future greater importance of this latest invader. The trees now in the open stands in depressions—as the pin oaks of the open sedgy pin oak consocies—are apparently the first trees to occupy the land on which they are growing. There is every indication that the complete closing in of forest is an act of the last century or two, that

previous to that time openings acres in extent were not uncommon in the till plain forest. Later successional development is demonstrable by existing communities; earlier stages are theoretical, based only on evidences offered by relic species and remnants of communities, by soil differences, and by secondary successions.

The earlier progress of succession (through herb and shrub stages) was extremely slow; later, with forest invasion, succession moved more rapidly; and again, with the establishment of late successional stages (white oak-beech) the progress again becomes extremely slow. The extremely slow development at first, later acceleration, and finally, extreme retardation of rate of change exhibited by these till plain successions is typical of successions in which progress depends on reactions of the vegetation, rather than on external change (Cooper, 1926).

Set-backs in succession due to catastrophe of some sort have occurred from time to time. Fire has always been a factor modifying succession. In these wet areas it is not often effective, though a number of areas burned over in recent years have been seen. The harmful effect on shrubs and saplings because of their superficial roots is most pronounced and may in some instances have eliminated certain shrub species.

Windfalls opening up small areas in the forest favor the intolerant species and sometimes account for the presence of occasional pioneer species in communities of advanced successional rank.

Grazing of wood-lots is all too prevalent. Very few areas can be found which are not being grazed or do not bear evidence of having been grazed in the past. This has resulted in more or less complete destruction of the characteristic herbaceous and shrub species and in injury to or destruction of saplings. It also has tended to compact the soil, destroy the lighter humus layer and thus change the water relations (Auten, 1933). *Polygonum acre* is a good grazing indicator.

Drought is a factor of extreme importance. The shallow root systems of many of the species make them susceptible to drought. The persistence in the area of more or less hydrophytic relic species (Braun, 1928) precludes the possibility of protracted dry periods affecting the entire area. Droughts of shorter duration, such as experienced in 1930, affect local areas. The drought of 1930 was severe enough to dry many of the depressions normally the wettest and hence most poorly aerated sites. In many such places, beech, and in a few places, white oak, were killed. Roots in these situations are nearer the surface, hence suffered greatly by the drying out of depressions. Sunny openings are thus created in the forest in areas which are generally wet. Small pin oak, red maple, and sweet gum are thriving; herbaceous plants, more or less suppressed but still present, multiply rapidly and grow luxuriantly. In this way, depression communities successionally much younger than the sur-

rounding forest or communities out of accord with the surrounding forest are produced. Some of the discrepancies in zonal arrangement and hence apparent anomalies in succession may be due to the effects of occasional droughts.

VI. SUMMARY

The forests of the Illinoian till plain of southwestern Ohio have been shown to be ecologically distinct from the forests of surrounding dissected areas. Occupying definite topographic sites favoring high soil water content and the formation of acid soils, the forests are, in their earlier successional stages, swamp forests. Only in the later stages are mesophytic conditions reached, and even then the characteristic species of the mixed mesophytic forest of southwestern and southern Ohio are lacking. The vegetation is co-extensive with the soil types on which it grows, soil types developed only in southwestern Ohio and southeastern Indiana. Similar soils in the Illinoian drift area of Illinois are drier and have developed under a drier climate; that region is climatically unlike the Ohio area, and its vegetation not similar to that of the Ohio area of Illinoian drift. Local areas of soils of similar color and moisture on the Cumberland Plateau support vegetation somewhat similar to that of the Ohio drift plains.

Climatic successions developing in the area have left their imprint on the present vegetation. A close correlation between forest communities and topography is evident and suggests the important rôle of soil water and soil aeration as causal factors in community distribution. Topography, however, changes but slowly, and the successions in progress are controlled largely by the reactions of vegetation—shading, competition, and modification of soil. The culmination of these successions leads to the establishment of a physiographic climax of distinctly more northern aspect and composition than the mixed mesophytic forest, the climatic climax of this geographic region.

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